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R THE BEHAVIOUR OF THE DESERT LOCUST (*SCHISTOCERCA GREGARIA* (FORSK.)) (ORTHOPT.) IN AN OUTBREAK CENTRE

By John S. KENNEDY, M.Sc., Ph.D.

(Communicated by Francis HEMMING, C.M.G., C.B.E., F.R.E.S.)

WITH PLATES 1 TO 9 AND 37 FIGURES.

(Read 1st March, 1939.)

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I. INTRODUCTION.

THE aim of this work is to add to knowledge of the behaviour aspect of phase transformation in the Desert Locust (*Schistocerca gregaria* (Forsk.)) in the field.

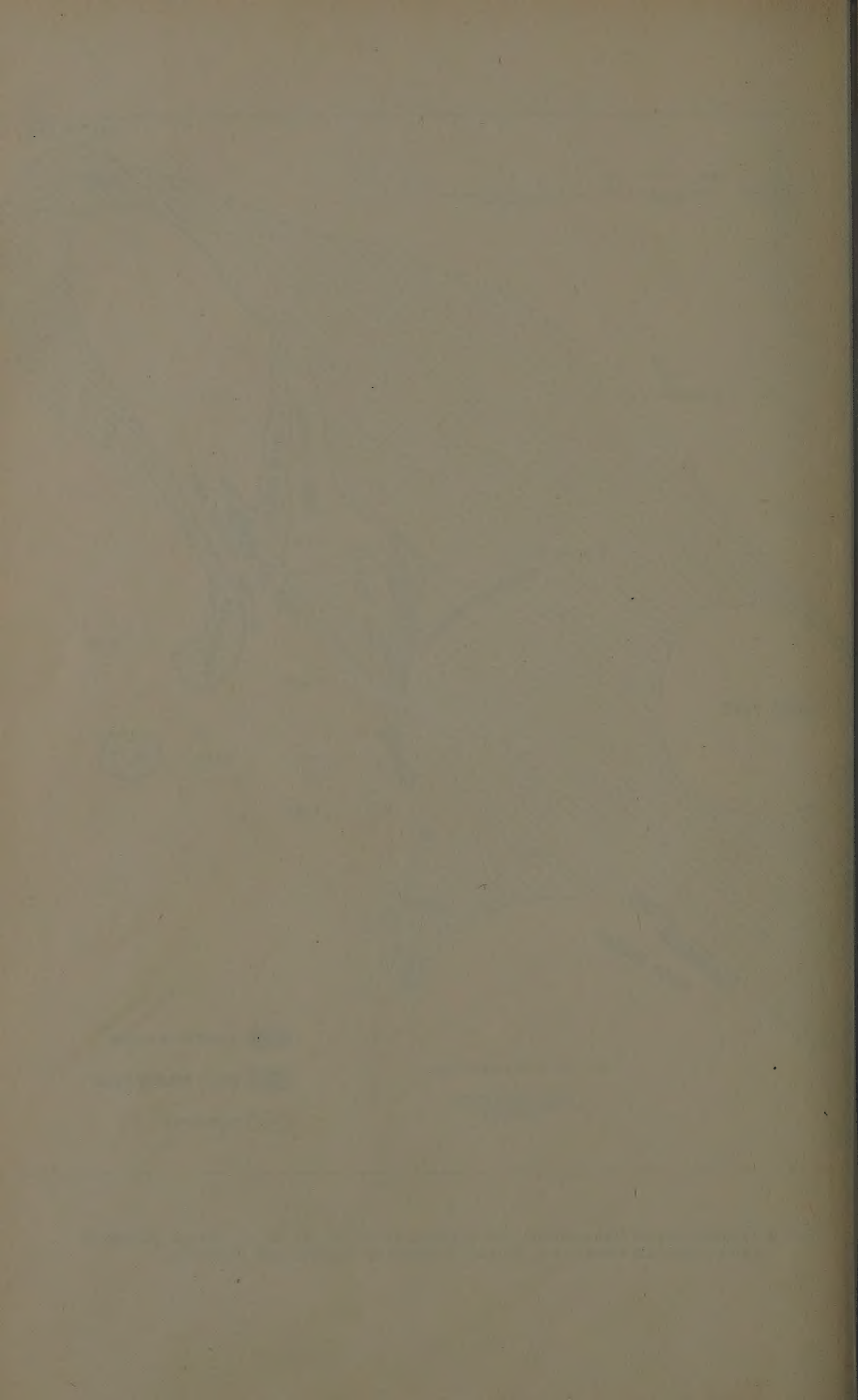
Uvarov's theory of phases in locusts advanced in 1921 is now generally accepted. This acceptance has meant that locust outbreaks are now regarded as involving not only an increase in numbers but the transformation of the whole appearance, structure and behaviour of the insects. In consequence field investigations have centred more and more on those regions where solitary

locusts live permanently. Phase transformation in *S. gregaria* has been observed by Johnston (1926) and Maxwell-Darling (1936) on the Sudanese coast of the Red Sea and elsewhere in other locusts by other observers. In the laboratory Faure (1932) and many others have induced phase transformation by crowding individuals of *solitaria* in breeding cages, and Husain and Mathur (1936) have demonstrated that single isolated individuals will assume gregarious coloration when artificially forced into activity.

Between field and laboratory findings there is, however, a considerable gap. There is little evidence that externally forced activity precedes crowding of individuals in the outbreak process in the field. This being so, it is assumed that crowding is necessary for the phase change in the field. In the laboratory crowding results from the bringing together of a number of individuals and the enclosing of them within the walls of a cage. It has been shown by Zolotarevsky (1933), Maxwell-Darling (1936) and others that substitutes for this crowding are provided in nature, but the processes have not been studied closely. In cage experiments, moreover, there has been nothing to prevent frequent contact between individuals, whereas in the field, concentrations are reported to occur in dense vegetation on which the locusts spend their life, so that frequent contact between the rather inactive individuals was difficult to imagine. This point appears to have received insufficient attention.

This work was, then, concerned mainly with the extent and causes of concentration movements, and the opportunities for intimate contact between individuals in concentrations. No attention was paid to the factors controlling multiplication. The whole period of the investigation (rather less than 4 months) was spent at one outbreak centre, Hamashiameb, on the Sudanese coast of the Red Sea. The length of this paper is due in part to the shortness of time and to the conditions prevailing. Much of the work was semi-experimental and is in urgent need of further laboratory tests; it is quoted here in the absence of any certainty that such tests are likely in the near future, and it has been necessary to allow impressions and speculations to play a considerable part.

My sincere thanks are offered to the many people whose assistance made the work possible: Sir Guy A. K. Marshall and the Imperial Institute of Entomology, who sponsored the investigation; Dr. B. P. Uvarov, whose idea it was and whose encouragement is much appreciated; Miss Z. Waloff for abstracting, translating and supplying literature from the Institute's Library; Dr. A. Bradford Hill and Dr. J. O. Irwin for advice on statistical matters; Dr. D. L. Gunn for helpful discussions; the Meteorological Office, London, for the loan of instruments; the Sudan Government, and in particular the Government Entomologist, Mr. H. W. Bedford, for generally smoothing my path and supplying an assistant; Mr. R. C. Maxwell-Darling for acting as guide, philosopher and friend in the early stages of my visit and for establishing the camp; the District Commissioner, Tokar, Mr. C. A. Lea, and the Agricultural Inspector, Tokar, Mr. R. Paterson, for much appreciated hospitality and their interest in the investigation; Sheikh Mustafa abu Zainab and his fellow-tribesmen of Hamashiameb, especially those known to me as Badani, "Sherif" and Mahomed Nur, for generous hospitality and willing co-operation at all times; Tawfic A. Khalifa Effendi for intelligent and enterprising assistance and self-sacrificing toleration of circumstances such as only those who have spent hours in a small covered pit under a tropical sun can appreciate; and to my wife for her very hard work and active interest in strange and uncongenial tasks both in the field and the preparation of this paper.



II. HAMASHIAMEB AND ITS VEGETATION.

The site of the investigation is mentioned (as Hamasheb) and shown on the map in Maxwell-Darling's paper (1936). For comparison with other outbreak centres on the coast reference should be made to that author.

Hamashiameb lies among sand dunes just outside the north-west edge of the Khor Baraka delta. Cultivation is not dependent on flood water from the hills (Maxwell-Darling 1936), but on direct rain and a flood flowing for a short distance over the coastal plain until soaked up by the sand. Cultivation consists almost exclusively of bulrush millet (*Pennisetum typhoideum* Rich.).

The large scale map (fig. 1) shows Hamashiameb and its environs, and some idea of the country may be got from pl. 1, fig. 1.

As may be seen from the map, the area comprises two distinct types of ground: the flat plain, usually of hard ground, and the masses of soft, shifting sand dunes, in which portions of the plain are partially enclosed as "khors." Hamashiameb and Wara Dibbab are two rather ill-defined areas separated by an arm of the dunes. Wara Dibbab was not studied closely, but in Hamashiameb rough outlines of the main vegetation zones (see below) are indicated. The dotted line shows the approximate course of the main flood in October 1936 (not shown at Wara Dibbab). Previously the main flood had reached the north end of Khor Toqwan and not entered the "Unnamed Khor" or the dunes towards Harabai Wells. In 1936, however, the dunes blocking the wide mouth of Khor Toqwan diverted much of the water, so that one branch of the flood entered the west opening of the Khor and reached the point shown, one branch forked left and penetrated far into the dunes towards Harabai Wells, and a third forked right and reached into the "Unnamed Khor." This largely determined the distribution of millet cultivation and other vegetation as shown on the map. In 1936 millet was planted for the first time in the "Unnamed Khor" and the dunes towards Harabai Wells, and much of Khor Toqwan was not cultivated for the first time. Apart from the dictates of soil moisture, soil nature determined the distribution of millet, which does best on soft non-clayey coarser soil and this is the reason millet was not planted throughout the course of the flood. Some millet, e.g. that near the Omargarab range, was dependent only on rain and was never as luxuriant as the rest.

For a description of the types of vegetation and the more common plants on the Red Sea coast reference is made to Maxwell-Darling (1936).

Vegetation varies with the season, and during the summer little but *Suaeda fruticosa* bushes survive. With the winter rains *Panicum turgidum* and *Cyperus* spp. appear and millet is sown. With millet a variety of annuals come up, chiefly grasses, but *Heliotropium pallens* is very common and, on the softer sand along the dune margins, *H. undulatum* also. The vegetation is most luxuriant at the end of December and beginning of January. After this the soil of the open plain, largely composed of fine silt and clay, begins to lose its moisture and the vegetation gradually dies. The sand dunes (where flooded) remain moist longest and millet planted on the coarse silt "floor" between the dunes remains green in patches until the beginning of April. Rain after the beginning of the year has very transient effects on the vegetation except among the dunes, where millet was re-sown after the rain at the end of January, and some weeds revived. By the end of April vegetation was rapidly approaching its summer condition and green millet was present only in one or two isolated patches among the dunes.

For descriptive purposes the vegetation may be divided into rough zones,

as they existed at the beginning of February. The classification is based mainly on the height and degree of horizontal continuity of the vegetation. It is not based on plant genera or type of soil, since, as appears below, locust distribution seemed to be correlated with vegetation density and hence with the amount of shelter from the almost incessant daily wind.

I. *Wind shelter negligible, or only as tiny "islands."* Less than 10% ground cover.

(a) Large areas of the plain (from entirely bare to covered with tiny tufts of grass, etc., and small bushes up to 30 cm. high and widely spaced). Pl. 2, fig. 2; pl. 4, fig. 6; pl. 9, figs. 17, 18.

(b) The sand dunes (large *Suaeda* or *Panicum* bushes up to 2.7 m. high and 4.5 m. across and about 30 m. apart, and occasional "mats" of *Heliotropium undulatum* among the marginal dunes. These "mats" constitute a special habitat, Ib'). The dunes consist of coarse loose sand continually moving under the influence of wind, southwards in the winter and northwards in summer. Pl. 2, fig. 3, and pl. 3, fig. 4.

(c) Portions of the plain and borders of the dunes in places. (*Suaeda* and *Panicum* bushes intermediate in size and spacing, between those in zones Ia and Ib. Ground vegetation rather better than in zone Ia.) Pl. 6, fig. 12 (foreground).

II. *Continuous but low wind shelter.* Almost 100% ground cover. (Usually dense grass but occasionally *Heliotropium pallens*, 15-30 cm. high, occurring in a few patches of the plain and particularly in Khor Toqwan.) Plate 3, fig. 5.

III. *Wind shelter very uneven, but ground cover usually over 80%.* (This zone comprises a great range of density of vegetation, formed of bushes, grasses, *H. undulatum* and *pallens*, etc., and occurs over considerable areas of the plain adjacent to the dunes.) Plate 4, figs. 6 and 7.

IV. *Continuous and high wind shelter.* Ground cover varies between 20% and 90%.

(a) A few portions of the plain (60-120 cm. high *Suaeda* bushes closely packed, some ground vegetation but bare ground interspersed. Ground cover about 85%). Plate 5, fig. 8.

(b) Millet cultivation among marginal dunes, or weeded cultivation elsewhere (little or no ground vegetation; ground cover about 20%. Among the dunes *H. undulatum* "mats" sometimes occur along the borders of the millet patches). Plate 5, fig. 9, and pl. 6, fig. 11.

(c) Unweeded millet cultivation on the open plain or within Khor Toqwan (density of undergrowth varying from thin grass or *H. pallens* to deep choking undergrowth including bushes). Plate 7, figs. 13 and 14; pl. 8, figs. 15 and 16.

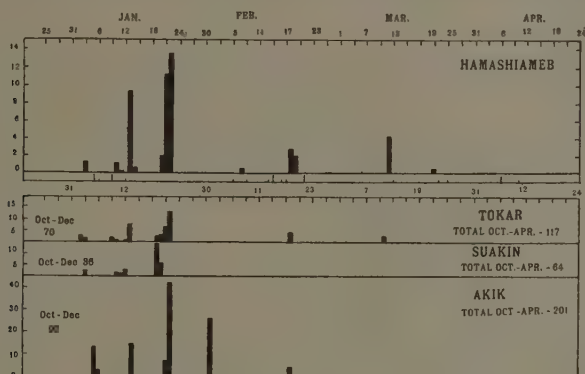
Whilst there exists every kind of intermediate density the above classification has a basis in fact. The least satisfactory is zone III, which passes imperceptibly into zone II, and zones IVa and IVc. Usually, however, millet cultivation (zones IVb and IVc) has well-defined margins and stands out in marked contrast to the surrounding vegetation.

III. WEATHER.

Maxwell-Darling (1936) has described the climatic conditions of the Red Sea coast and my remarks are therefore confined to the peculiarities of the winter season 1936-37.

Rainfall.

The main rains and flood occurred at Hamashiambeb towards the end of October 1936 according to local inhabitants. The rain all fell during one night. Rainfall records for the period of the investigation are shown in fig. 2, with figures for other stations in the southern part of the Sudanese coastal strip. The rainfall in this period was greater, especially in January, than in the same period in 1935 when Maxwell-Darling was at Khor Ashat. He found few of the first winter generation adults becoming sexually mature, so that the second winter generation was small and no outbreak occurred. Figures for Ashat and Hamashiambeb are not available except for the winters of 1934-35 and 1936-37, respectively, and it is therefore difficult to make comparisons, especially as no data are available for Hamashiambeb during the earlier winter months of 1936. Fig. 1 shows that rain fell at about the same time at



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FIG. 2.—Rainfall at Hamashiambeb and three other places on the same coast, during the period of the visit.

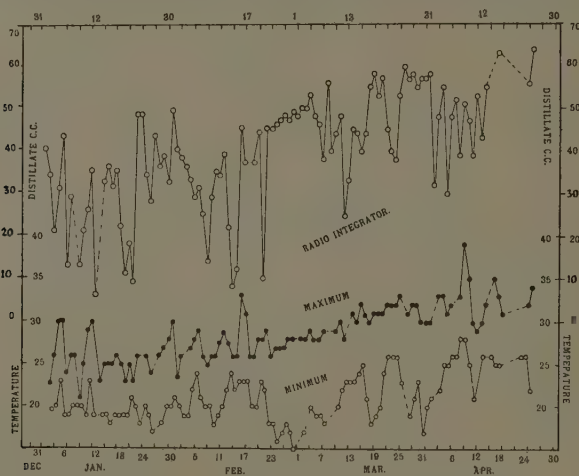
Tokar and Hamashiambeb, although the former always received less; Tokar is farther from the hills and sea. The Tokar figures, which are available for all recent years, may be used as an indication of conditions on that part of the coast during outbreak and non-outbreak years. Maxwell-Darling (1936) gave the winter rainfall (fig. 3) at Tokar and other places from 1904 to 1935. The total rainfall at Tokar in October 1936–April 1937 was 117 mm., whereas in the same period 1933-34 it was about 150 mm. and unusually high also farther north beyond Ashat at Suakin and Port Sudan. It was in the 1933-34 season that Maxwell-Darling observed the production of a second winter generation and incipient swarming at Ashat. This suggests that the expectation, based on rainfall, of an outbreak at Hamashiambeb in 1937 was less than in 1934. At the same time it appears that the expectations at Hamashiambeb in 1937 were better than at Ashat in 1935, when no considerable second generation was produced.

Fig. 1 also shows that rain fell at Suakin at roughly the same times as at Hamashiambeb and Tokar, but was less and ceased earlier. At Akik, about 50 miles south of Hamashiambeb near the sea, rain fell at quite different times.

There was no outbreak at Akik in 1936-37 when the total rainfall for October-April was 201 mm. (only 92 mm. fell before January), whereas in 1935 there was an outbreak (Maxwell-Darling, 1936) when the total rainfall was over 280 mm. and the bulk fell in November.

Air temperature and humidity.

Fig. 3 shows the daily maximum and minimum temperatures in the standard screen, and the amount of distillate in a Wilson Radio Integrator during January, February, March and part of April. Fig. 4 shows the monthly averages from 2-hour readings of a thermohygrograph in the standard screen in the same period. The humidity data for January, shown in fig. 4, apply



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FIG. 3.—Daily readings of the maximum and minimum thermometers in the standard screen, and of the volume of distillate in the Wilson Radio Integrator.

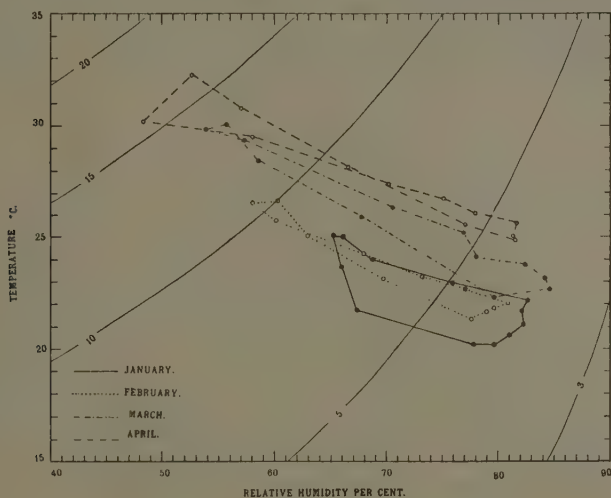
only to the latter half of the month as the hygrograph was not working properly before that. Fig. 4 emphasises the generally high humidity typical of coastal stations, and it is striking that although daytime humidity falls as the season advances and temperatures rise there is little variation in night humidity from January to April.

The daily average screen humidity calculated from the hygrograph record in the standard screen at Hamashameb was higher in January and February and slightly lower in March than in a screen 7 inches (17.5 cm.) off the ground in the same months of 1935 at Ashat, when Maxwell-Darling found no general sexual maturation among first winter generation adults.

The Wilson Radio Integrator is a glass bulb, exposed to the sun, containing a black suspension in spirit, and leading to a graduated tube enclosed in a perforated white box below. The amount distilled over is no more than an indication of the total solar radiation during that day. The bulb was not

enclosed and therefore subject to the cooling effects of the wind. Moreover, the amount of distillation depends not only on the heating of the exposed fluid but on the difference in temperature between the fluid and the air surrounding the shaded receiving tube below. Unless the bulb is enclosed *in vacuo* and the air temperature fluctuates little, no calibration in terms of radiant energy received is possible. The Radio Integrator may nevertheless be regarded as an indicator and the figures obtained emphasise the great daily variation in intensity of solar radiation. The gradual increase in volume of distillate is due not only to the change in the sun's position as the season advances but also to the gradual reduction in cloud.

Cloudiness is an important climatic factor. Loose clouds, formed over the sea, are carried inland and gradually mass in great banks as they approach



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FIG. 4.—Average two-hourly readings of a thermohygrograph in the standard screen. Lines representing equal saturation deficiencies (gm./m.³) are included.

the hills. Cloudless days are very rare. Not until March are days with many continuous hours of sunshine common. Cloud over Hamashiameb is not, however, usually in a continuous sheet and sudden changes in intensity of radiation are frequent.

The wind is no less important. There is scarcely a day without a moderately strong wind. Wind was measured (with an airmeter) on most days only once and not always at the same time. Occasionally the wind strength and direction was taken at intervals throughout the day; these readings are given below (figs. 10 and 22). The strongest wind experienced during the visit was in January, when the average velocity in the morning was over 7 m./sec. In February, March and April it was about 5 m./sec. During the night there was usually little or no wind; it rose shortly after sunrise and dropped about sunset. It blew mainly from the north during January and February, sometimes veering north-east later in the day. In March and April it came usually

from the north in the early morning and evening, but veered north-east and east, and sometimes south, during the day. The windiness of coastal stations is important to locusts in many ways as it accentuates micro-climatic differences between zones of different vegetation density.

IV. LOCUST POPULATIONS.

Johnston (1926) discovered in February 1926 that the Red Sea coast of the Sudan was an area where *S. gregaria* could be transformed from the solitary to the gregarious phase. In subsequent years this process may have continued, but it was obscured by the migrant swarms of the great outbreak of 1925-1931 using the area as a winter breeding-place. Swarms were last reported there in the winter 1931, since when no fully gregarious swarms were seen until the new immigration of December 1936. In 1933-34 and 1934-35 incipient outbreaks were observed by Maxwell-Darling (1936), in whose paper further locust history is given for the Sudanese coast.

TABLE I.

Changes in locust populations of Hamashiameb, October 1936-April 1937.

		Indigenous		Immigrant	
		Hoppers	Adults	Hoppers	Adults
October	End		" Old " ovipositing.		
November	Beginning	First seen.			
	Middle		First " new " seen.		1st swarm.
December	End				Ovipositing.
	Beginning				
January	Middle			Hatching from 1st swarm eggs.	
	End	Max. nos. of		Poisoning of above.	
	Beginning	4th and 5th instar. No new appearing.	Max. nos.	All destroyed.	2nd swarm. Oviposition. Most gone.
February	Middle	All 5th instar.			3rd swarm. All gone.
	End		Only a few soft ones left.	Hatching from 2nd swarm eggs. Most marched away;	
	Beginning	Last seen.		many stragglers left.	
March	Middle		Fewer still, but hard.	All 5th instar.	
	End		Sexual maturation starts.	Last seen.	First F ₁ from 2nd swarm.
	Beginning				Max. no. of F ₁ . 10% only left.
April	Middle		All (in cages) with large eggs.		Very few left.
	End				Yellowing in cages.

1. *Sequence of Events during 1937 Visit.*

During the spring 1937 visit to Hamashiameb an indigenous population, more or less solitary in phase, and an immigrant, more or less gregarious, population were present. The changes in population during the period are shown in Table I. "Old" adults are those surviving from the previous winter breeding season, "new" adults are the first winter generation, offspring of the "old." In spite of the mixture of populations it was always possible to distinguish indigenous from immigrant locusts.

(a) *Indigenous populations.*

On my arrival (end December) indigenous hoppers, especially in the younger instars, were numerous. Very few "old" adults were found, but new adults had begun to appear in fair numbers. These could be distinguished from the old by being lighter in colour, softer and with no eggs visible in the ovaries. By the end of January new young hoppers ceased to appear and 4th and 5th instar hoppers were at their maximum. In the latter half of February numbers of hoppers had decreased considerably and all were in the 4th or 5th instar, mainly the latter. The last indigenous hoppers were seen at the beginning of March. The number of new adults increased during January but the maximum was seen at the same time as that of the older hoppers (end January-beginning February). At the time a rough estimate of 2000 individuals seen was made in the course of a walk of 5 minutes through the main cultivation at Khor Toqwan. After this, adults surprisingly decreased, it being expected that the peak would come after that in numbers of hoppers. The marked reduction was also noted during this period at other places in Hamashiameb and at Wara Dibbab. Moreover, the majority of the adults found at the beginning of March were not properly hardened and without visible eggs in the ovaries, whereas those caught at the end of January and kept in cages were fully hardened, and in some visible eggs had appeared. During the first half of March the number of hard adults caught dwindled almost to none, those caught being all recently moulted. By the middle of March hard ones began to reappear, the softer ones ceasing to be caught. All this seems to indicate that at some time after the beginning of February indigenous adults had emigrated as fast as they hardened enough to fly, and that the emigration had decreased considerably about the beginning of March, so that individuals moulting to adult at that time remained at Hamashiameb after hardening. During the latter half of February comparatively little time was spent in the cultivation, and neither individual nor mass emigrations of indigenous adults were observed. It should be mentioned that at this time the second immigrant swarm was working through the cultivation, and loose flights were leaving daily for a week.

By the middle of March only 50 indigenous adults were seen in Khor Toqwan in a walk of 20 minutes, *i.e.* one one-hundred-and-fiftieth part of the numbers seen at the beginning of February. Most individuals collected in mid-March had ovaries with eggs just becoming visible. Towards the end of March the proportion increased till it became the overwhelming majority, and, in a minority, eggs had reached about half-size. At this time *dissocians* adults predominated more and more and indigenous adults could only be seen in cages. These, dissected in the third week of April, all had large eggs and one egg-pod had been deposited. It seems, therefore, that a second winter generation at Hamashiameb in 1937 was possible, if the new adults issuing

during January and February had not disappeared, seemingly by emigration, possibly stimulated by the passing swarm.

(b) *Immigrant Populations.*

On my arrival at Hamashameb the first immigrant swarm had been established about a week. The swarm, flying low and raggedly, came apparently from the south-south-east, *i.e.* the general direction of Tokar. The cotton cultivation between Tokar and the hills, in the upper parts of the Khor Baraka, had previously been invaded by swarms of uncertain origin (probably Eritrean), and immigrants into Hamashameb were apparently detachments from the main swarm. Similar detachments were found all over the coastal area between Khor Ashat and the Tokar delta in the early months of 1937. The first Hamashameb swarm was probably only a few thousand individuals restricted at first to cultivation in the "Unnamed Khor," but gradually dispersed throughout the main cultivation in January, leaving many eggs in the "Unnamed Khor." Hatching of hoppers began on 15th January; it began suddenly and intensively at all points and may have been provoked by the first serious rain for several weeks (over 9 mm.) which fell on the 13th. Hatching continued for several days and poisoning was soon started and resulted in almost complete destruction before many hoppers had reached the 3rd instar. On 7th February there was a new invasion by a larger, but again loose, low-flying, swarm, from the same direction. This swarm did not remain, and after a week all but a few stragglers had moved off to the north in loose, straggling flights. Whilst in Hamashameb, however, they laid innumerable eggs throughout the area, including Wara Dibbab. Mass hatching started on 19th February, again immediately after the first appreciable rainfall during the embryonic period (2.7 mm. on the 18th, 2.0 mm. on the 19th). The primary bands soon coalesced to produce bands covering many square metres, and marching began two days later. For the first three days all bands marched northwards, the vanguard reaching the end of Khor Toqwan. After that their direction changed, most abandoning Hamashameb marching with the wind, south-south-west towards the hills, and they were largely exterminated before becoming adult. Considerable numbers of stragglers were left everywhere in thick vegetation, so as to repopulate the whole cultivation with fresh hoppers; the last indigenous hoppers were seen at the beginning of March. In the clean millet in the mouth of Khor Toqwan, sufficient gregarious hoppers remained to retain their band-formation and wander about. Poisoning of these hoppers re-started later, but they were already becoming adult; these and the isolated hoppers left behind elsewhere, became *dissocians* and the adults formed no swarms.

The maximum number of *dissocians* adults was present at the beginning of April; by the 6th, however, numbers had decreased to about 10% of what they had been on the 3rd. In this case there was little doubt that emigration had occurred, so rapid was the disappearance of the locusts. Again, however, emigration was not actually observed and there was no passing swarm to "pick up" the sedentary locusts. The remainder continued slowly, but steadily, to decline in numbers until by the end of April few remained. Caged individuals began to show signs of sexual maturation (yellowing of the body) at the end of April, but the eggs were still very small. On 16th February a third loose and low-flying swarm passed from west-south-west to east-north-east through Hamashameb, but did not stay for more than a day and laid only a few eggs at Wara Dibbab and the southernmost Hamashameb cultiva-

tion. A few hoppers hatched from these eggs about 8th March. In this case no rain fell except at the outset of the incubation period; this probably accounts for the longer time before hatching. The subsequent fate of these hoppers was not observed.

2. Coloration.

(a) *Indigenous Populations.*

The great majority of the young hoppers were entirely green, but, as they become older, brown to black markings appeared in many individuals, despite the absence of marching or other signs of heightened activity. Even when well developed, the markings were somewhat irregular, and the bow-shaped mark on the pronotum typical of gregarious hoppers was seldom clear. There is never much pigment on the head in general or the mouth-parts in particular; the latter are particularly well pigmented in gregarious or *dis-socians* hoppers, even if other parts of the head be lighter in colour. The brown eye-stripes always stood out clearly from the straw-coloured background. Fifth instar hoppers were the best pigmented; the maximum extent and intensity was as shown by Husain and Mathur (1936, pl. xxxv, fig. 5). The background was still, however, a good grass-green, as was the general body colour of all-green hoppers, of which a typical example is shown (with rather a darker green) in Husain and Mathur (1936, pl. xxxiv, fig. 5). Faure (1932, pl. xix, fig. 53) shows a *solitaria* hopper with the body colour distinctly yellower than those at Hamashameb. A few of the black-marked individuals showed a yellower background, such as in Faure's fig. 55 or Husain and Mathur's pl. xxxv, fig. 5.

To estimate the incidence of dark pigmentation in the field, three main grades were fixed arbitrarily: first, pure grass-green hoppers in which the sub-ocular wedge was often distinctly blue and the maximum development of blackness a thin line ("anterior muscle impression" of Husain and Ahmed, 1936) on the hind femur as in Faure's fig. 53; second, intermediate conditions where the black pigment was present on the hind femora both as the anterior muscle impression and as two small patches on the upper surface and on the distal head, on the posterior dorsal surface of the pronotum, and segmentally along the dorsal surface and to a lesser extent the lateral surfaces of the abdomen; and third, examples approximating to Husain and Mathur's pl. xxxv, fig. 5, in extent of black pigment, *i.e.* in the sub-ocular wedge, on the lateral as well as on the posterior dorsal surfaces of the pronotum, as above but better developed on the hind femora, on the proximal and distal ends of the hind tibiae, on all the tarsi, on the sides of the meso- and metathorax, on the veins of the elytra, and in a well-developed pattern on all abdominal segments, but never showing much darkening of the antennae. A fourth category was made, to include examples with the yellower background of Husain and Mathur's pl. xxxv, fig. 5, which appeared quite distinct, and so far as black was concerned fell either into the second or third categories above. In Table II is shown the proportion of individuals falling into the four categories in five field collections.

The "old" sexually mature indigenous adults were dirty grey with no definite pattern. Their offspring, on becoming adult, were at first generally cream-coloured with a greyish or greenish tinge; as they hardened the skin darkened, and a clear pattern was apparent in a few hours. The head and legs showed little pattern nor did the abdomen except a hopper-like pattern in fresh-moulted individuals. The pronotum and other segments of the thorax showed well-defined dark brown to black markings, and on the former two

TABLE II.
Coloration of hoppers.

Collection			No. in collection	% in coloration categories			
Date	Place	Vegetation zone		1	2	3	4
4.ii.	Wara Dibbab.	III	51	45	37	10	8
19.ii.	Main cultivation Khor Toqwan.	IVc	88	26	33	40	1
20.ii.	N. end of Khor Toqwan cultivation.	II	16	69	13	18	0
20.ii.	N. end of Khor Toqwan cultivation.	IVb	53	51	40	9	0
22.ii.	Extreme N. end of Khor Toqwan cultivation.	IVc	135	56	29	14	0

dark stripes ran along the dorsal surface, narrower and denser in front, fanning out and less dense posteriorly. The dark stripes were spotted with the lighter colour of the general body background, the spots being very fine in the anterior halves but larger (though still smaller than in *dissocians* adults) in the posterior halves. Small dark marks were usually present on the sides of the pronotum. The general body colour was rather indeterminate, varying between light iron grey and dirty fawn or cream. In addition to these colours adults showed varying amounts of pink suffusion, usually better developed in the males. Sometimes the pinkness was visible only in one or two places such as the lighter parts of the pronotum or the anterior tibiae, but sometimes the whole thorax and legs showed a fairly deep, pink suffusion. Pinkness was never found on the white hind-wings and almost never on the abdomen. The degree of pinkness of the adult was connected with that of dark pigmentation in the hoppers. Seven pure green, and seven of the blackest, hoppers were put in separate cages, and it was found that adults from the latter were appreciably pinker on average than those from the former. There was no appreciable difference in the average E/F ratio of the two sets of adults.

At the beginning of February about a third of the adults caught showed well-marked pinkness on the legs and body, and about two-thirds some tinting of the tibiae. By the beginning of March practically all showed some degree of pinkness; this did not increase in adults caught and caged earlier, and its increase in the field is attributed to the increased blackness of hoppers as the season advanced. The eyes of all indigenous adults were light-coloured between the stripes.

By mid-March in caged adults, and in some degree in field catches, pinkness began to disappear and the whole body became more unicolorous, the black pronotal stripes fading. The hind-wings began to show faint yellowness in about 10%, and first signs were apparent on the body of one or two examples. Out of 44 examples dissected 2 showed medium-sized, and the rest very small, eggs. During the latter half of March the pinkness and dark pattern continued to disappear and yellowness on wings, pronotum and abdomen to develop clearly. During April, caged individuals became more or less unicolorous dirty fawn- or grey-yellow, while the eggs enlarged and had reached full size when the remaining females were dissected in the third week of April, when all, particularly males, were yellow coloured.

The initial pinkness and subsequent yellowing of the body with sexual maturation is sometimes regarded as a distinguishing feature of the gregarious phase of *S. gregaria* not found in solitaries (Telenga, 1930; Maxwell-Darling, 1934). Inhabitants of an outbreak centre probably may not be regarded as true *solitaria*, but these observations and those of Maxwell-Darling (1936), Ramchandra Rao (1936b, 1937c) and Volkonsky (1938) show that yellowing can take place in "sedentary" near-solitary populations.

(b) *Immigrant populations.*

Members of the first immigrant swarm had the typical coloration of sexually mature phase *gregaria*, a rich yellow-ochre suffusion over the whole body, and dark mahogany-coloured eyes in which stripes were not discernible. The yellowness was much better developed than in the yellowest of the indigenous adults at the end of April. Members of the next two swarms were similar in colour. It was remarkable that up to 30% of the hoppers hatching from the eggs laid by the first immigrant swarm were green coloured even several days after hatching. Subsequent changes were not observed as the hoppers were soon poisoned, but the greenness of so many suggested that the swarm was recently formed.

Hoppers hatching from the eggs laid by second and third immigrant swarms, except a few individuals, were all black pigmented in typical gregarious manner. The offspring of the third set of immigrants were not studied, but those of the second were observed in many places and changes of colour noted. Members of the marching bands which left Hamashameb were typical in colour. The hoppers left in the cultivation were not examined closely until the later instars, when they showed varying degrees of *transiens* (*dissocians*) coloration. There were two main types: hoppers in bands remaining in the clean millet until becoming adult and those separated by the undergrowth from their fellows since the 1st or 2nd instar. Hoppers in the bands were not so dark as Husain and Ahmad's (1936) pl. xxxvii, fig. 4, or Faure's (1932) fig. 55, but were intermediate in colour between the former's pl. xxxvi and xxxviii, fig. 4. General body colour was light fawn with an orange tint, the eyes not as shown in Husain and Ahmad's pl. xxxvi, the stripes not standing out so clearly. Remains of the uniform mahogany eye-colour, typical of phase *gregaria*, appeared in the posterior part of the eye so that only the anterior stripes were more or less well defined. The head was usually surrounded by a complete "bandage" of black. The antennae were dark. The pronotum was seldom entirely black, this colour tending to disappear at the sides. On the hind femora the "anterior muscle impression" was always joined to the two dorsal patches. Coloration of isolated hoppers varied greatly, none showing as well developed a pattern as the above; the black tended to become dirty brown and the general colour was not the grass-green of solitaries even when no dark pigment was present, but a yellower, more golden green as in Faure's fig. 53 (1932). The antennae were usually dark. None of the hoppers had a complete head "bandage," but where black pigment was present some was usually to be found on the mouth-parts. None showed the bluish sub-ocular wedge sometimes found in green solitaries. The eyes always, even in pure green hoppers, showed a trace of the dark background in the posterior half of the eye. It appeared that the mahogany of *gregaria* eyes is lost in *dissocians* from the front backwards. When the pronotum showed any dark pattern this was usually present only antero-laterally and postero-dorsally. The anterior muscle impression on the hind femora was seldom joined to the dorsal marks.

Hence it was concluded that black-marked or green *dissocians* could be distinguished from similar *solitaria* or *congregans* hoppers by the remains of brown pigment in the eyes, by the darker antennae and the yellower body background of the former, and by their being livelier and more "alert" (see p. 521).

Adults derived from the above *dissocians* hoppers were taken during the latter half of March with indigenous adults. Immature individuals of both were generally similar in appearance but almost always distinguishable. Adult *dissocians* usually showed remains of brown background colour posteriorly in the eyes (never present in indigenous adults). Pinkness on the body was definitely more marked in *dissocians*. The dark stripes along each side of the dorsal surface of the pronotum were "dappled" with appreciably larger spots. These last two differences can probably not be used unless both types be examined together, but the remnants of dark colour in the eyes may be of use.

Towards the end of April *dissocians* adults showed signs of sexual maturation, wings and body becoming yellow, and it was sometimes difficult to distinguish them from indigenous yellowing adults, but the yellow of maturing *dissocians* and indigenous adults was less extensive, lighter and less amber-tinted than in members of flying swarms.

3. Measurements.

Measurements of length of femora and elytra were made on indigenous adults, on some of the first immigrant swarm and on *dissocians* adults (offspring of the second immigrant swarm). All measurements were made with dividers and a metal scale on freshly killed specimens.

The average ratios (calculated as average E divided by average F) of males and females in the various collections are shown in Tables IIIA and IV with

TABLE IIIA.

E/F ratios of A. locusts indigenous to Hamashameb, B. other solitary *Schistocerca* (from Maxwell-Darling (1934)).

Collection			♂♂		♀♀	
No.	Place	Date	No.	E/F ratio	No.	E/F ratio
1	Wara Dibbab.	16.i.	44	2.066	50	2.044
2	Khor Toqwan.	7.ii.-3.iii.	50	2.052	69	2.070
3	Khor Toqwan.	13-15.iii.	45	2.053	43	2.044

TABLE IIIB.

Population	Date	♂♂		♀♀	
		No.	E/F ratio	No.	E/F ratio
Libyan Desert	1932	—	—	6	2.09
"F" Um Darag	ix.1932	100	2.05	100	2.11
"H ₁ " Khor Arbaat (F ₁) . .	ii.1934	54	2.07	37	2.08
"P ₁ " Khor Ashat (F ₁) . .	ii.1935	80	2.08	79	2.10
"L" Hamashameb (F ₂) . .	v.1934	60	2.11	60	2.13

some figures given by Maxwell-Darling (1934, 1936). The mean ratios for the different collections of locusts indigenous to Hamashiameb in 1937 are similar and the three collections are placed together in fig. 5A, which shows the frequency distribution of the ratios. Maxwell-Darling (1934) regarded the Um Darag population ("F") as "*solitaria* for all practical purposes," and the Libyan Desert females as more extreme *solitaria*. Ramchandra Rao (1936c) regards as *solitaria* ratios below 2.05, as *transiens* 2.06-2.15, and as *gregaria* over 2.16, and Zolotarevsky and Murat (1938) describe as "typical *solitaria*" ratios in Mauritania, 1.97 for males and 2.03 for females. Maxwell-Darling's Red Sea coast populations, including one at Ashot in a non-outbreak year, have higher E/F ratios than my indigenous population. Moreover, my females had even lower E/F ratios than the so-called "extreme *solitaria*" from the Libyan Desert. Nevertheless other evidence such as black markings on hoppers, pinkness and subsequent yellowing of adults and the unstable condition of the Red Sea coast populations, suggest that the 1937 Hamashiameb population was not extreme *solitaria*.

When considering immigrant populations (Table IV) further peculiarities appear. All ratios are lower than those Maxwell-Darling and Ramchandra Rao regard as typical of *gregaria*, even lower than in Maxwell-Darling's "very small mature swarm" from the Red Sea coast.¹

TABLE IVa.

E/F ratios of A. locusts immigrant into Hamashiameb, B. other gregarious *Schistocerca* (from Maxwell-Darling (1934)).

Collection			♂♂		♀♀	
No.	Place and particulars	Date	No.	E/F ratio	No.	E/F ratio
1	"Unnamed Khor." 1st, small mature swarm.	3.i.	50	2.000	50	2.003
2	Open plain. Moulded in crowded cages from gregarious hoppers from marching bands. (Offspring of 2nd, large swarm.)	28.iii.	16	2.132	8	2.221
3	Khor Toqwan. Moulded in cages from stationary bands of <i>dissocians</i> hoppers. (Offspring of same.)	8-10.iv.	56	2.092	42	2.148
4	Khor Toqwan. Moulded in cages from extreme green <i>dissocians</i> not in bands. (Offspring of same.)	23-31.iii.	9	2.133	12	2.110

The collections listed in Table IVa fall in two sets, the first small immigrant, and the *dissocians* offspring of the second larger swarm; the frequency distribution of the E/F ratios of these two sets are given in fig. 5. The first immigrant swarm has an unprecedentedly small E/F ratio, not only lower than that of the *dissocians* adults, but than that of the indigenous or "extreme *solitaria*" population. Care was taken to make the measurements exactly according to instructions (*Proc. 4th int. Locust Conf.* (1937) and

¹ This is true even if the ratios be obtained by the other method (not recommended by the fourth International Locust Conference, 1937) of averaging individual ratios.

Zolotarevsky (1933)) so that mistakes in method seemed to be excluded. Offspring of the second immigrant swarm retained a similar E/F ratio regardless of their degree of association during hopper life.

TABLE IVB.

Population	Date	♂♂		♀♀	
		No.	E/F ratio	No.	E/F ratio
"Mature swarm" Wad Medani . . .	1930	130	2.27	68	2.32
"Very small mature swarm" Red Sea coast . . .	xii.1931	45	2.24	92	2.31
"Fairly young swarm" N. Kordofan . .	xii.1931	24	2.23	22	2.27

Further comparison of the indigenous, first immigrant, and offspring of second immigrant populations in terms of absolute lengths of elytra and femora, and of differences in these lengths between the sexes, is made in Table V. The differences between the size differences in the sexes of indi-

TABLE V.

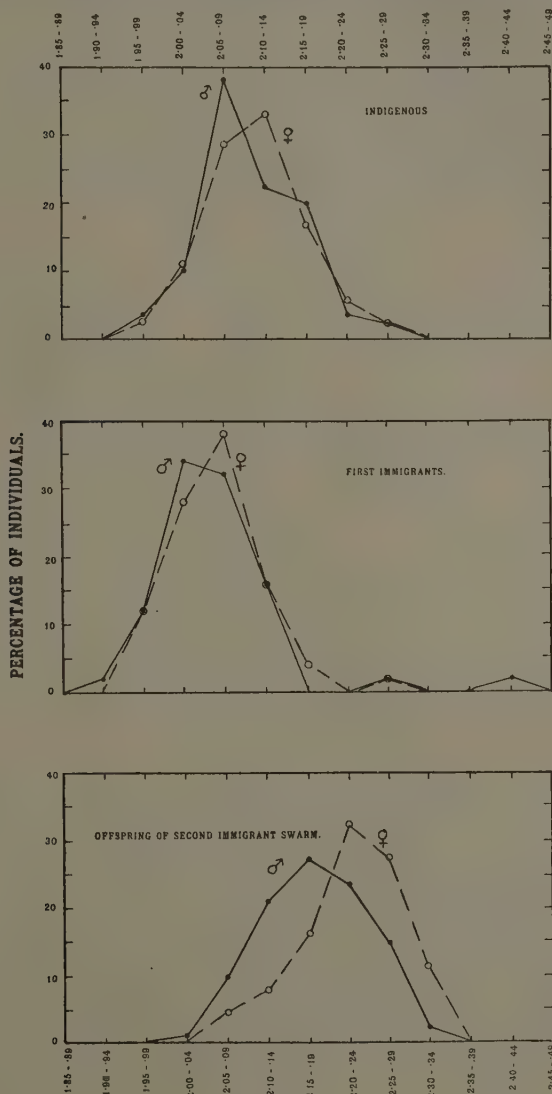
Comparison of dimensions of the three populations measured at Hamashameb.

Populations compared		Differences within the same sex				Differences between sexes	
		♂♂		♀♀		♀♀ minus ♂♂	
		E	F	E	F	E	F
Indigenous minus 1st immigrants.	Mean sizes (mm.) Difference S.E. of difference.	51.061 54.300 -3.239 ±0.3635	24.946 27.100 -2.154 ±0.1673	60.401 63.440 -3.039 ±0.3766	29.333 31.640 -2.307 ±0.2131	9.339 9.140 +0.199 ±0.4915	4.387 4.840 -0.453 ±0.5863
Indigenous minus offspring of 2nd immigrants.	Mean sizes (mm.) Difference S.E. of difference.	51.061 49.167 +1.894 ±0.3635	24.946 23.142 +1.804 ±0.1828	60.401 55.323 +5.078 ±0.9931	29.333 25.048 +4.285 ±0.2673	9.339 6.256 +3.083 ±0.6538	4.387 1.906 +2.481 ±0.6082
1st immigrants minus offspring of 2nd immigrants.	Mean sizes (mm.) Difference S.E. of difference.	54.300 49.167 +5.133 ±0.3990	27.100 23.142 +3.958 ±0.1806	63.440 55.323 +8.117 ±0.5292	31.640 25.048 +6.592 ±0.2835	9.140 6.286 +2.854 ±0.4073	4.540 1.906 +2.634 ±0.3362

genous and first immigrant populations, are not significant. All the other differences shown in the table are so much larger than their standard errors that they can hardly be attributed to chance. On the basis of this table the three populations may be placed in the same order as that of their average E/F ratios: the first immigrant swarm most "solitary," the indigenous population intermediate, and the *dissocians* offspring of the second immigrant swarm nearest to *gregaria*. Offspring of the second immigrants have shorter elytra and femora than indigenous locusts, while the latter have shorter elytra and femora than the first immigrants. Similarly these organs of the females are longer, relative to those of the males in both indigenous and first immigrant populations, than in the offspring of the second immigrants.

These facts (if attention be confined to biometric data, and the first immi-

grants being a swarm be ignored) are in general accord with other findings (Zolotarevsky, 1929; Lean, 1936; Zolotarevsky and Murat, 1938; Johnston, 1937). Firstly it is apparent that behaviour and colour changes go in advance

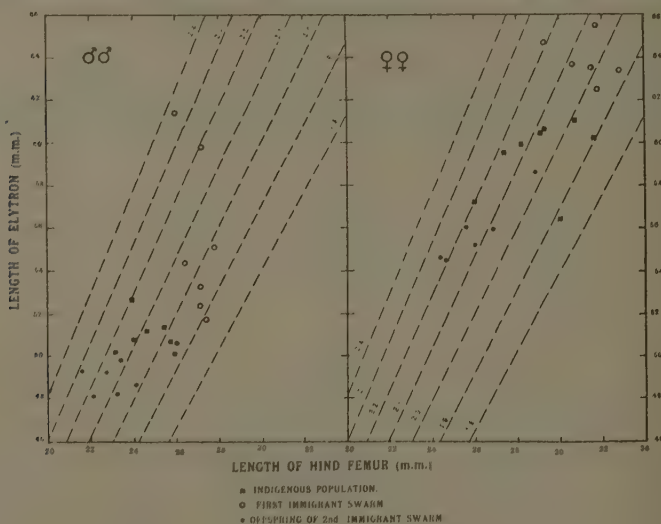


5

FIG. 5.—Frequency distributions of E/F ratios of the three populations of locusts measured. Indigenous, 139 ♂♂, 162 ♀♀; First Immigrants, 50 ♂♂, 50 ♀♀; offspring of second immigrants, 81 ♂♂, 62 ♀♀.

of biometric changes on a short-term basis, and secondly this seems also true on a longer term basis. The swarms observed on the Sudanese coast in 1937 were the first of a new outbreak still (spring 1938) gathering momentum. The swarms of which Maxwell-Darling (1934) gave E/F ratios were part of a prolonged outbreak drawing to its close. The lower E/F ratio of the 1937 swarms may probably be attributed to this difference. Lespes, Regnier and Rungs (1930) found members of invading swarms of *S. gregaria* at first predominantly of the *solitaria* type, subsequent swarms containing more and more individuals with full *gregaria* appearance.

Thus it seems that the E/F ratio and other biometric features are unsafe criteria of phase unless account be taken of the stage of given individuals in the whole cycle of outbreak and non-outbreak years, covering many genera-



6

FIG. 6.—“Phase graphs”; for explanation see text.

tions. A population which appears a fully gregarious swarm may be biometrically “solitary” if it comes among the early swarms of an outbreak and *vice versa*, apparently solitary locusts may be biometrically “gregarious” if they appear at the end of an outbreak period. Similarly Lean’s (1936) or Zolotarevsky’s (1938) criteria for distinguishing *congregans* from *dissocians* in *Locusta migratoria migratorioides* R. & F. may be found to vary with the stage in an outbreak at which the examples studied begin to “dissociate.”

Lean (1936) found fruitful suggestions in the construction of “phase graphs,” in which average clytral length is plotted against average femoral length, for each group of individuals whose E/F ratios fall within each 0.05 interval in the range of E/F ratios present. This is done for the 1937 Hamashianeb populations in fig. 6. It shows the size differences mentioned above, but the points do not fall on curves of consistent shape as in the *Locusta* populations studied by Lean.

The data obtained do not help in the problem of distinguishing biometrically phase *congregans* from *dissocians*. Lean (1936) and Zolotarevsky (1938) reached different conclusions with regard to *Locusta*, but the origin of Zolotarevsky's populations is more certain, and in his opinion sexual dimorphism is greater in *congregans* than *dissocians*. Sexual dimorphism in both the indigenous and first immigrant populations at Hamashameb was certainly greater than that of *dissocians* offspring of the 2nd immigrants (Table V), but the indigenous population was probably only just becoming *congregans*, the first immigrants while certainly *congregans*, except biometrically, had an extremely solitary E/F ratio, therefore neither was strictly *congregans*. Possibly *Schistocerca* is more indefinite and plastic than *Locusta* in its phase differences (cf. Volkonsky, 1938.)

4. Summary.

1. The indigenous population of Hamashameb passed through only one generation in winter 1936-37.

2. The maximum of young hoppers was at the end of December and of older hoppers and adults end January.

3. With hardening of the skin adults disappeared rapidly, possibly by individual emigration stimulated by a passing swarm.

4. Indigenous hoppers included many with dark or brown pattern, especially in later instars.

5. Indigenous adults showed distinct traces of pinkness when immature, and yellowness when mature.

6. These adults were biometrically *solitaria*, but otherwise incipient *congregans*.

7. Three invasions by mature swarms took place in December and January.

8. The first swarm was small and lacked impetus to leave Hamashameb again, and was biometrically very "solitary." Many hoppers hatching from eggs from this swarm remained green until destroyed in the 2nd instar.

9. The second swarm was larger and left after a week, having laid many eggs.

10. Hoppers from these eggs were typical *gregaria*; most marched off in large bands and were destroyed.

11. Many gregarious hoppers remained in the cultivation to become *dissocians* in varying degrees. They were distinguishable from indigenous hoppers even after they had lost all dark pattern.

12. Adults from *dissocians* hoppers lived solitarily but were distinguishable by their appearance, high E/F ratio and other biometrical features.

13. Adult *dissocians* were at first numerous but in three days decreased by 90%, almost certainly by emigration, although this was not observed.

14. Conclusions that biometrical changes lag behind colour and behaviour changes in the phase cycle were confirmed and more evidence adduced that this applies as well on a long, as a short, term basis.

V. LOCUST BEHAVIOUR.

Foreword.

The first full description of the outbreak process is by Zolotarevsky (1933, 1934a), for *Locusta migratoria capito* Sauss. in Madagascar, where the important rôle of concentration and multiplication of individuals is brought out.

As stated in the Introduction, concentration alone cannot produce an outbreak, since *solitaria* could not meet sufficiently closely and frequently in the field, even in dense, crowded, populations, to cause the actual change of phase.

There are thus, I believe, three stages in the outbreak process which it is desirable to distinguish in theory and are, I hope, justified in practice. They may be defined as follows :—

1. *Concentration*; the absolute increase of population density in a restricted area. This may be produced by (i) active centripetal movements into the area; this may be termed *real concentration*, or (ii) by localised breeding causing crowding of new generations from the outset without the aid of active migrations; this may be termed *virtual concentration*. Both are to be distinguished from *apparent concentration*, the result of differences in local survival rates and irrelevant to the outbreak process.

2. *Aggregation*; the grouping of concentrated individuals in contact with each other so that fellow-individuals assume an increasingly important part in the sensory experience of each locust.

3. *Gregarisation*; the change of phase (appearance of gregarious behaviour and coloration), the result of intensive aggregation.

From Maxwell-Darling's account (1936) the decisive, but not the only, factor in the causation of an outbreak of *S. gregaria* on the Red Sea coast, is the Virtual Concentration produced by a 2nd generation in one winter season.

In accordance with the above definitions, observations at Hamashiameb in 1937, and references to the work of others, are arranged under the headings *Concentration* and *Aggregation*. In the absence of an outbreak *Gregarisation* was not observed and remarks on this process are therefore speculative.

As the centre of interest was behaviour, observations on "sedentary," solitary-living *dissocians* are included under *Concentration* and *Aggregation* of indigenous populations where thought permissible.

A. CONCENTRATION.

1. Hoppers.

(i) *Distribution of hatching sites.*

Before considering possible concentration movements, information on the distribution of hatching sites, and therefore of oviposition of the "old" adults, is desirable. Unfortunately oviposition was almost completed and some hoppers had become adult before I arrived.

The question, therefore, can be approached only from consideration of the soil requirements of females ready to oviposit and the distribution of soil to suit these requirements; of the old adults at the beginning of the season; and of the young hoppers, in the belief, probably true (Maxwell-Darling, 1936), that these hoppers are inactive and do not wander.

There is no direct evidence on the distribution of adults in October before flood water descends and millet is planted. Maxwell-Darling's first figures are for November, when cultivation had apparently begun. Locusts were then most numerous in cultivation, although about half as many could be found where cultivation had been the previous winter.

In April and May the annual vegetation is largely dried up and vegetation density is not marked at Hamashiameb. In the summer this process advances further and it may be assumed that locusts surviving this period become

more scattered than in the winter. That scattering is limited to a few hundred metres from the previous year's cultivation is suggested by indigenous hoppers being found in 1937 only very rarely in the eastern half of the plain of Hamashiameb near the Omagarab dune range, in the "Unnamed Khor," in the millet in the dunes towards Harabai Wells, or in the eastern half of Wara Dibbab, although in all these places suitable oviposition sites were abundant.

Locusts must, however, have been present in the northern arm of Khor Toqwan at the beginning of summer, for cultivation was plentiful there in the winter 1935-36. The soil did not remain moist on the surface long, although moistened by rain, since flood water did not reach here in October 1936, so that there was less oviposition than in places soaked by flood; in any case, adults probably soon moved to the more abundant vegetation of the flooded area to the south-west. Hoppers were not in fact found in the northern arm. As is shown below, this had little to do with lack of cultivation or of *H. undulatum* in the 1936-37 season as far as these factors might drive young hoppers away.

These facts suggest that the distribution of main hatching sites, while different from and more extensive than that of the resulting adults, is limited by distribution of the older adults (near the previous year's cultivation) and the course and extent of the flood water. According to Maxwell-Darling, furthermore, oviposition is repeated and continuous and many eggs are laid after the millet and other vegetation had sprung up, and thus the concentration tendencies of the adults would help concentrate eggs in the area of green vegetation along the course of the flood.

There is some published information on the soil requirements of females ready to oviposit. *Schistocerca* is more selective than *Locusta* in the texture and moisture content of the soil (Johnston and Maxwell-Darling, 1931). Bareness of ground seems essential, and fairly soft, medium moist, coarse, sandy or silty soil is chosen by solitaries if available (Maxwell-Darling, 1934; Ramchandra Rao, 1936a). Swarms have been recorded ovipositing under stones, in dry or soaked sand, or even on the surface, in the absence of optimum conditions (Bodkin, 1930; Bodenheimer, 1930; Galperstein and Moritz, 1930; King, 1930), but normally, hard, dry, soaked or clayey ground is avoided.

It does not suffice to know the soil requirements of the female without knowing her means of finding suitable soil when available, and how far solitary females will search, if distribution of eggs is to be deduced satisfactorily; nothing is at present known on this point.

Suitable oviposition sites were actually very widespread and frequent. Most of the plain at Hamashiameb, subjected to repeated floods, consists of clay and fine silt in layers as deposited in successive years. This was almost certainly unsuitable for oviposition and females were never seen to oviposit in it, but except in the areas marked "bare" on the map, this "floor" had everywhere mounds of looser, sandier soil, and the dunes were always surrounded by a border of blown sand many metres wide. Blown sand entered Khor Toqwan in the southern portion below the constriction marked on the map, but north of this it was often hard and clayey. The best and most used oviposition sites were among the marginal dunes, where the rapidly-drying surface layers are repeatedly removed by the wind. Not only was this so on open windward slopes, but also in relatively sheltered ones exposed to spasmodic gusts and eddies. These places were in fact those chosen by females both for "basking" and oviposition.

It is provisionally concluded, considering the probable distribution of old

adults and suitable soil, that most eggs were laid along the course of the flood (except where this was more than a few hundred metres from the previous year's cultivation, and in a few places where the soil was unsuitable), but especially on the borders of the dune ranges, and probably hoppers hatched over the same area, large in relation to those where older hoppers and adults were subsequently most abundant. The distribution of hoppers at the beginning of January confirmed this.

(ii) *Distribution of hoppers.*

At the end of December and beginning of January hoppers were numerous in zones II, III, IVa and IVc, provided that the vegetation lay within 200 metres of the dune ranges and a shorter distance of previous cultivation, and on the "mats" of *H. undulatum* in the marginal dunes. None was found elsewhere in zone Ib proper. Hoppers were rare in zone Ic, but 4th and 5th instars were moderately common in zone IVb.

Many counts of indigenous hoppers were made in January and February, by selecting a plot of approximately uniform vegetation type and one man catching as many hoppers as possible in 10 minutes without moving more than was necessary. Distribution was studied on a very small scale and the difficulty of adopting a consistent technique will be appreciated when remembering the great patchiness of the vegetation. Because of the correlation between density of vegetation and difficulty of capture the density of vegetation also affected the results. In the Circular Trench Experiments (see below) known numbers of hoppers were introduced into previously unpopulated patches of vegetation and then counted. From these counts and impressions in the field it was estimated that in really dense, uneven vegetation, e.g. zones IVa and IVc, probably less than 20% and nearer 10% are captured, more in less dense vegetation, and almost 100% in very sparse vegetation such as zone Ia.

These figures, with the estimated area on which a count was made, were used to give an approximate population per square metre:—

$$\text{Population Density (no. per sq. metre)} = \frac{N \times C}{A}$$

where N = no. taken, A = area of count in square metres, and C = factor for the variation in difficulty of capture. C is taken as:—

10 for zones IVc and IVa.

4 for zone II.

2 for zone III (denser kinds).

1.4 for zones III (thinner kinds) and IVb.

1 for zones Ia and Ic.

Intermediate values of C were used where necessary. The values of C above are for later instar hoppers, for younger hoppers the value would be much higher, but the difficulty of seeing and catching them was so great that no attempt was made to estimate them separately. Figures for them are nevertheless included in the calculations, since time spent in catching young hoppers would otherwise have produced older hoppers. The results of counts are given in Table VI, from which several suggestions emerge as they do from general observation of distribution where no actual count was made.

1. The importance of vegetation density, particularly ground vegetation, was immediately apparent, e.g. the population was not at all dense in clean

millet unless planted so thickly as to be equivalent to ground vegetation (comp. count G, 10.ii., with counts in clean and unweeded millet). I am unable to agree with Maxwell-Darling (1936a) that *H. undulatum* is a necessary constituent of habitats with dense populations. *H. pallens*, which is nearly related, is common in undergrowth but it is not essential (see count C, 23.ii.). This area was of particular interest as both species were present within a few metres of it (D and E, 23.ii.), and yet population density was nearly 4 times as great in C as in any nearby area. At Wara Dibbab (27.i.) hoppers were more numerous on the *Suaeda*-bearing mounds, with or without *H. pallens*, than between the mounds where it was often abundant (it was absent in count A). *H. undulatum* was not present on, or between, the mounds. Both examples typify well the phenomenon that vegetation density provides a better indication of hopper abundance than do the species of plants present.

It must be emphasised, however, that relative, not absolute, vegetation density was the key to hopper distribution. Near unweeded millet cultivation, hoppers were most numerous in the millet (H and J, 10.ii.; E, 20.ii.; C, 23.ii.), but in some parts of Wara Dibbab (5.i. and 27.i.) and Hamashameb (10.i.) really dense vegetation such as unweeded millet was not nearer than many metres, and hoppers were always most numerous in the densest available vegetation (D, 5.i.; B, 27.i.; C, 10.i.).

2. Differences in distribution of younger and older hoppers were apparent.

Even when plentiful, no real attempts were made to take 1st or 2nd instar hoppers, and most observations on these are qualitative.

Firstly, young hoppers were almost invariably found in close proximity (2 or 3 m.) to good oviposition sites, as were older hoppers usually, but not always. For instance, count B, 5.i. was on hard clayey ground over 30 m. from the softer sand at the edge of the dunes, and older hoppers were found in such places not uncommonly.

Secondly, differences in distribution of young and older hoppers in relation to density of undergrowth were pronounced. As stated above, hoppers of all ages were most numerous in the thickest vegetation available, but it was noticeable for older hoppers to be found (although in smaller numbers) in vegetation with undergrowth that was not the densest available. This is shown by counts on 5.i., but was especially noticeable in millet. Even entirely "clean" millet always had a certain number of older hoppers, if hoppers were at all common and despite the presence of dense undergrowth near by (e.g. counts E, 1.i.; C and D, 10.ii.; C, 20.ii.; and 23.ii.). On 5.i., for instance, while most hoppers in count D were young, numerous older ones were also found in the adjoining unweeded millet.

Thirdly, where dense undergrowth was available both in, and adjoining but outside the millet, young hoppers were found both inside and outside, the older ones mainly inside. For instance, at Wara Dibbab on 5.i., most of count D (*H. pallens* clumps) were young, but in adjoining unweeded millet, count E, older hoppers were also present.

The counts on 20.ii. are particularly interesting. The thickest ground vegetation available was dense grass (A) which had supported a considerable population of young hoppers, but now that these were most in the later instars, a denser population was found along the south edge of the grass just before millet cultivation began. Further in the millet, weeds and a still denser population were found. Consideration of these counts suggests that D acted as a trap for older hoppers wandering off the dense grass (counts A and B). D could not be classified as clean millet or dense grass, as it was on the border line. Doubtless

TABLE VI.
Counts of hoppers.

Sym- bol	Vegetation zone and particulars	Remarks	Instars	No.	" Cor- rected " No. per m. ²
1.I. In the middle of the cultivated part of Khor Toqwan. All counts within 50 metres of each other.					
A	IVc. Small <i>H. undulatum</i> mat in unweeded millet.		Mostly 4th and 5th caught, many younger present.	16	7.5
B	IVb-c. Dense clump of <i>H. pallens</i> in cleaner millet.		As A.	21	8.4
C	II. Large patch almost pure <i>H. pallens</i> .		Mostly 4th and 5th present.	22	1.8
D	II-IVc. Strip of <i>H. pallens</i> along border between dense grass and weeded millet.		All.	27	9.0
E	IVb. Weeded millet adjoining D.	On bases of millet stands.	4th and 5th only.	38	1.1
5.I. At Wara Dibbab. A, B and C near and along the east side of the extreme south-west point of the Wara Dibbab range of dunes. D adjoining B (which was similar to pl. 8, fig. 16).					
A	III. Small <i>Suaeda</i> bushes, <i>H. pallens</i> and grasses, against margin of dunes.	Mostly on <i>H. pallens</i> .	All <i>H. pallens</i> .	18	1.0
B	III. Small <i>Suaeda</i> bushes, thinner <i>H. pallens</i> , 40 m. from dunes.		4th and 5th only.	16	0.5
C	Ia-c. Smaller scattered bushes and <i>H. pallens</i> , 10 m. farther from dunes than B.			0	0
D	II-III. Dense masses of <i>H. pallens</i> adjoining dune margin and cultivation.		Mostly 1st-3rd.	78	6.1
E	IVc. Unweeded millet with small bushes, <i>H. pallens</i> and <i>undulatum</i> and grasses.		All.	58	11.6
10.I. Between the camp and Khor Toqwan. 200 m. east of nearest cultivation among vegetation similar to but intermediate in density between pls. 4, fig. 6 and 5, fig. 8. All counts immediately adjacent.					
A	III. Small mounds bare except for occasional <i>Suaeda</i> bushes up to 60 cm. high.			0	0
B	III. Low ground between mounds, scanty <i>H. pallens</i> , grass, and bushes.	On <i>H. pallens</i> and smallest bushes.	2nd-4th.	10	0.5
C	III. 50% cover of <i>H. pallens</i> and grass, <i>Suaeda</i> up to 1 m. high.		2nd-5th.	19	3.8
D	III. Smaller mounds than A with 30-cm. bushes, very thin <i>H. pallens</i> , grass, etc.	On bare ground between bushes.	4th and 5th.	13	2.6
27.I. At Wara Dibbab. Pl. 4, fig. 7 shows exactly similar terrain, except that no <i>H. pallens</i> was present between the mounds where the counts were made. All counts adjacent to each other.					
A	III. 8-cm. grass carpet between mounds.		Mostly 5th.	22	0.2
B	III. On small mounds surmounted by <i>Suaeda</i> and with <i>H. pallens</i> thinly at the sides. Some grass.		Mostly 4th and 5th.	87	10.9
C	III. On similar mounds but with less vegetation apart from <i>Suaeda</i> .		Mostly 5th.	34	2.9
10.II. A-I (inclusive) in and around the comparatively clean millet in the southern half of the Khor Toqwan cultivation. Each plot contiguous with the next in the order given, and all within 100 metres of each other.					
A	Ia-b. Between millet and fixed dunes. A few <i>Suaeda</i> and <i>Panicum</i> bushes up to 80 cm. high. Very scarce ground vegetation.			0	0
B	Ic. New-sown millet 60 cm. high, very thin grass cover.			0	0
C	Ic-IVb. Thin grass and <i>H. pallens</i> and a few 1.5 m. millet stands.		1 5th, 4 4ths.	5	0.5
D	IVb-c. Unweeded millet, but generally thin.		4 5ths, 2 4ths.	6	0.1
E	IVb. Thick millet, clean except for a few thin <i>H. pallens</i> clumps.	All on <i>H. pallens</i> .	6 5ths, 2 4ths.	8	0.3
F	IVb-c. Thick millet, some thin <i>H. pallens</i> , grass, etc.	All on <i>H. pallens</i> , some 5th on millet.	8 5ths, 4 4ths, 2 3rds.	14	0.6
G	IVb-c. Extremely thick millet, no weeds.		6 5ths, 7 4ths, 2 3rds.	15	0.9
H	IVc. Medium thick millet, thick irregular undergrowth.	On undergrowth and small groups on ground.	12 5ths, 10 4ths, 5 3rds, 7 2nds.	34	6.8
I	Ic-IVb. 1 m. millet stands, not dense, weeded previous day.			0	0

TABLE VI (continued).

Sym- bol	Vegetation zone and particulars	Remarks	Instars	No.	"Cor- rected" No. per m. ²
10.II. In and around the unweeded millet in the northern half of Khor Toqwan cultivation. K and L contiguous. J within 20 m. of K and L, M and N 100 m. north of K.					
J	IVc. Millet with thick undergrowth (pl. 7, figs. 13 and 14).	Most on bare patches.	8 5ths, 14 4ths, 10 3rds.	32	6.4
K	Ia-II. Thin grass carpet on soft sand against dune margin.	In grass.	1sts.	8	0.5
L	II. Uniformly dense grass between K and millet, with small scattered bushes.	On grass.	16 2nds, 4 1sts.	20	1.6
M	II. Small patch of uneven grass and <i>H. pallens</i> between dune margin and millet.		7 5ths, 9 4ths, 3 3rds, 12 2nds, 9 1sts.	33	4.1
N	II. Patch of dense grass 10 m. wide in midst of dense unweeded millet.			0	0
10.II. 80 metres from nearest millet in the uncultivated western wing of Khor Toqwan.					
O	IVa. Uniformly dense grass and numerous thick <i>Suaeda</i> bushes up to 1.2 m. high.	5ths on bushes, others in grass.	5 5ths, 7 4ths, 12 3rds, 3 2nds, 2 1sts.	20	5.8
20.II. In and around the unweeded millet just south of and adjacent to the large patch of dense grass in the northern part of the Khor Toqwan cultivation. A, B, C and D mutually contiguous, E contiguous with O.					
A	II. Dense grass close to dunes, few thin millet stands, some bare patches.	Most on bare patches.	6 5ths, 5 4ths, 4 3rds, 1 2nd.	16	1.6
B	II-III. Similar to A but no millet and grass less deep and less continuous; small scattered bushes.	Most on bare patches.	4 5ths, 5 3rds.	9	0.7
C	IVb. Thick weeded millet.	On ground but not in groups.	18 5ths, 8 4ths, 3 3rds.	29	0.2
D	Along the border between thick grass (B) and weeded millet (C).	Grouped on ground, shelter of grass margin.	13 5ths, 6 4ths, 5 3rds.	24	6.4
E	IVc. Thick unweeded millet (similar to 10.II. H).	Grouped on bare patches.	18 5ths, 13 4ths, 14 3rds, 2 2nds.	47	9.4
23.II. In and around the strip of very dense vegetation forming the northern limit of the cultivation in Khor Toqwan, separated from the main cultivation by a large patch of dense grass (23.II. counts) A, B and C contiguous, passing away from the dunes in that order. D contiguous with A on the east; E south of A.					
A	II-III. Uniformly dense grass, scattered bushes up to 1.2 m. high, few scattered millet stands (pl. 8, fig. 5).		All 5th.	3	0.1
B	IVc. Transition zone between A and C.	On millet and on bare patches.	18 5ths, 8 4ths, 2 3rds.	33	2.3
C	IVc. Very dense irregular vegetation forming a strip 5 m. wide invaded by arms of the dunes; thick 1.8 m. millet, deep grass, large <i>Suaeda</i> bushes up to 2 m. high, bare patches interspersed.	Grouped on bare patches.	17 5ths, 9 4ths, 6 3rds.	32	8.8
D	Io-III. Transition zone between C and an adjacent zone Io area. Thin <i>H. undulatum</i> and grasses, one or two bushes.		3 5ths, 4 2nds.	7	0.1
E	IVc. Thick millet, few <i>Panicum</i> bushes, patches of grass and sparse <i>H. undulatum</i> .	Young on grass, older on ground.	6 5ths, 4 4ths, 2 2nds, 5 1sts.	17	1.1

most of the day was spent "basking" on the bare ground sheltered from the north wind along the grass margin, and the night in the grass. Such observations require that the statement that dense vegetation is the most important concentrating factor for older hoppers be corrected, since combined with some bare ground it is probably more effective than a continuous carpet of undergrowth. In Hamashameb in 1937, when hoppers were in later instars, large expanses of continuous grass (zone II) were fairly rare, so that they did not play a big

part in determining the presence or absence of interspersed bare ground patches, as they may in some circumstances (see Johnston and Buxton, 1937, on *Locusta*).

3. In correlation with the differences in distribution of young and old hoppers suggesting a greater mobility in later instars, the distribution of hoppers was seen to change with the advance in the season and the change of most hoppers to later instars. Owing to these changes the counts do not show the steady decrease in the total of hoppers in Hamashiameb in January and February. Apart from adverse climatic effects, the number and range of predators appeared very great, birds, foxes, hedgehogs, mice, lizards, snakes, toads, scorpions, ants, and predacious beetles being seen eating hoppers. Nevertheless older hoppers increased in the millet. For instance, hoppers appeared first in any numbers in the relatively clean millet west-north-west of the camp at the beginning of February, while in the near-by zone III area, with much denser undergrowth, hoppers had mostly disappeared.

In the rather special case of "mats" of *H. undulatum* among the marginal dunes, parallel observations were made. Younger hoppers were numerous but older hoppers became less so and reappeared in near-by millet.

No direct observations were made, but it is likely that Maxwell-Darling (1936) assumes correctly that the considerable, but spasmodic and patchy, weeding of the millet, alters the distribution of hoppers and concentrates them, since clean millet is never densely populated if ground vegetation is available near by.

TABLE VII.

Changes in distribution of locusts of various stages.
0, none; 1, rare; 2, few; 3, some; 4, many; 5, most.

Vegetation zone	Hoppers		Adults	
	Young	Older	Recently moulted	Older
Ia	0	0	0	0.5
Ib	0	0	0	0.5
<i>Heliotropium</i> mats . .	5	2	1	0.5
Ic	0	1	1	1
II	4	3	3	2
III	5	4	4	3
IVa	4	4	4	4
IVb	2	3	3	4
IVc	4	5	5	5

Table VII shows the changes in distribution as the hoppers became older. Consideration of the table and the map shows that places where older hoppers were most numerous were more restricted than those where young hoppers were most numerous.

This suggests that young hoppers were relatively inactive and wandered no farther from the hatching sites than the nearest ground vegetation. Older hoppers seemed to scatter more, to be dependent, but less so, on the thick ground vegetation and to spread into the millet even if the undergrowth was no denser than elsewhere near by.

The questions arise as to what factors condition the movements of hoppers; why is dense undergrowth so important; what is the significance of bare ground

interspersed in undergrowth; and why does millet, as such, act as a concentrating agent.

(iii) *The food factor.*

The importance of the food factor in distribution and movements of hoppers is obscure. Maxwell-Darling (1936) ascribes in large part the distribution and movements of young hoppers of the 1st winter generation to the presence of *H. undulatum*, assuming that this is preferred by the hoppers as food, but I cannot support this claim.

Before deciding the rôle of a plant in concentration, it must be known not only that it is preferred to others in cages, but if it is not immediately available, by what means is it found, whether the preference is strong enough to cause the rejection of others and protracted wandering and, lastly, whether, preference or no preference, survival or development rates are different on other food-plants.

Direct attraction (presumably by smell) to *H. undulatum* can probably be ignored as of no importance, since it could only apply upwind, despite Lépiney's (1930b) statement that *S. gregaria* hoppers are attracted by the smell of crushed leaves of *Asphodelus*, treacle and arsenic bran, and to each other. There is a tendency on open, but not on well-covered ground, for hoppers to move upwind. The influence of smell is thus greater than it would be otherwise, but in inactive young hoppers smell seems of small importance.

Observation of hopper distribution showed no decisive preference for *H. undulatum* or the related and commoner *H. pallens*. A rough 4-day qualitative experiment was carried out in cages in January on food preference of 5th instar hoppers. Twenty-five were caged with a food jar with approximately equal-sized sprigs of various plants arranged radially in water. The water was

TABLE VIII.

Results of experiments on food preference of hoppers.

1, largely eaten; 2, about half eaten; 3, slightly eaten; 4, nibbled; 5, untouched.

Plant	1st day	2nd day	3rd day	4th day
A <i>Heliotropium undulatum</i> .	1	1	1	1
B <i>Heliotropium pallens</i> .	3	2	1	1
C <i>Pennisetum typhoides</i> .	2	2	2	2
D <i>Aristolochia bracteata</i> .	5	4	2	3
E <i>Euphorbia</i> sp.	3	5	3	2
F <i>Cenchrus</i> sp.	4	5	3	3
G <i>Suaeda fruticosa</i> . . .	5	5	4	5

inaccessible. Notes were made daily, at the renewal of the plants, of the extent to which each had been eaten and the results are given in Table VIII. The order of apparent preference is also that of apparent water content, except that the salt-bush *Suaeda* has very fleshy leaves.

The few results merit little attention, but there are some points of interest. A, B, and C were eaten consistently, especially A. Gregarious hoppers, marching through cultivation at Hamashiameb, stripped the *H. undulatum* mats, but damaged the millet relatively little. Whilst possibly a food preference, the stoppage of the hoppers by the mats due to their mechanical "braking" effect has to be considered. G was scarcely touched, D, E, and F only to an intermediate extent, B, D, E, and F were eaten very variably, but while such variations would presumably cancel out in a long series of experiments, they are

of interest, for if food preferences were sharp probably only *H. undulatum* or *H. pallens* would be eaten. Since no high selectivity was shown when the whole series of plants were offered, it is difficult to escape the conclusion that hoppers would be far less selective in the field.

Suaeda fruticosa is rejected by the hoppers even at the cost of life (see below). In this case food "preference" probably affects distribution and movements, including those of the earliest instars. Edney (1937) has shown clearly that lack of food in *Locusta* (causing hunger, or thirst, or both) increases activity, possibly as soon as 2-2½ hours. It is probable that some hoppers hatch in places where the nearest vegetation is *Suaeda*, for while *Suaeda* is not eaten by the adults their daily movements may take them some way from other plants. In this case hoppers would probably first climb the *Suaeda* and later, stimulated by hunger, descend and wander until they find millet or *H. undulatum*.

Karandikar (1933a) and Ramchandra Rao (1937c) have described experiments on food preferences of *S. gregaria* hoppers. 1st and 2nd instar hoppers from a Pasni "rek" (Baluchistan) preferred *H. undulatum*, but the grasses, *Pennisetum cenchroides* and *Eleusine flagellifera*, were eaten considerably, and other plants to less degree (Karandikar, 1933a). "Black" hoppers "of various stages" from Mekran reks ate various plants in the following order: *Zea mays*, *Pennisetum typhoideum* equal first, then *Cyperus arenarius* and *H. undulatum* equal, *Andropogon sorghum* next, and *Sericostoma pauciflorum*, *Aerua javanica*, and *Sphaerocoma hookeri*, very little eaten (Ramchandra Rao, 1937c). Observations in India confirm that preference is a matter of freshness and commonness of the plants. For instance, Ramchandra Rao (1937c) states that on the Western reks *H. undulatum*, *Aerua javanica* and *Cyperus arenarius* are most eaten, on the Eastern reks (where *Heliotropium* is scarce) *Sericostoma pauciflorum*, *Aerua javanica* and certain grasses, and in Sind-Rajputana *Indigofera cordifolia*, *A. javanica*, *Tribulus terrestris*, *Cyperus* sp., *Cenchrus catharticus*, and *Tephrosia* sp. It is probable that these differences are due less to adoption and adaptation of semi-fixed food preference habits, than to the normally polyphagous habits of *S. gregaria*.

Johnston and Maxwell-Darling (1931) state that *Locusta* is very selective in feeding habits on the Red Sea coast, whereas "the larvae of *S. gregaria* . . . fed on a wider range of plants and were not at all geophilous." Uvarov (1928) says ". . . food-preferences are observed, however, only when there is a possibility of choice, but when the preferred plants are absent, the same species may feed on many others, not even avoiding those that are directly poisonous."

It is possible that hoppers, with or without marked preference, do not do so well on some plants as on others, thus causing local differences in survival rates, and so Apparent Concentration. An experiment was carried out on this point, but was inconclusive as few hoppers could be spared. Twelve millet-fed hoppers were placed in each of 6 cages, and the number alive noted daily for 10 days. In cage 1 with no food, 8 died by the 3rd day and all by the 5th; in 2, with *Suaeda*, 9 were dead in 5 days and 1 more on the 10th day; in 3, with *Cenchrus setigerus*, 4 hoppers had died by the 10th day; in 4, the *H. pallens* cage, only 2 died by the 7th day but 4 more by the 10th; in 5, with *H. undulatum*, 1 had died by the 7th day but 5 more by the 10th; in 6, with millet, 2 had died by the 3rd day and no more by the 10th. The experiments were quite inadequate and inconclusive in the differences between cages 3, 4, 5, and 6. The higher death rate on *Suaeda* is significant; they did not attack it till the 5th day and even on the 10th less was eaten than on the other plants.

Experiments are known showing differences in rate of hopper development according to food-plant (Ramchandra Rao, 1937c). Presumably Real Concentration would be accelerated by growth-stimulating foods such as *H. undulatum*, as more mobile later instars would be reached sooner. Growth-stimulation could also assist Virtual Concentration, but probably only by contributing towards the fitting of second generation into a winter season.

The influence of food on hopper distribution and movements is still not clear, but it is tempting to regard food as a factor of minor importance, but not negligible. Whatever effects may be attributed to it, it does appear to account for hopper distribution and the main movements composing the process of Real Concentration. These movements of older hoppers and adults (see below) were into denser vegetation whatever its composition, and particularly into millet. There is little evidence of strong preference for millet as against plants often outside millet such as *Heliotropium* spp. or *Cyperus*. Wherever hoppers are likely to hatch in an area such as Hamashameb there is a plentiful supply of nourishment which the hoppers consume readily both in nature and captivity. In fact food supplies may be abandoned if other conditions are unfavourable.

This view is not exceptional, although contrary to Maxwell-Darling's (1936). It is possible that *H. undulatum* was the commonest weed at Ashat at the time of Maxwell-Darling's observations, both among the dunes and cultivation, and an appearance of preference was given, whereas other weeds were at least as common at Hamashameb.

After studying the ACRIDIDAE of Lake Chad, Golding (1934a) said (1934b) "the graminivorous species of Acrididae are not monophagous, and their choice of stations appears to be influenced by micro-climatic conditions rather than by the nature of the vegetation itself." Grassé (1929) also considered vegetation important as a physical factor rather than as food. There appears good reason to assume that such considerations apply to *S. gregaria*.

(iv) Observations on hopper movements

Attention was centred on the comparative rates of travel of the older hoppers on different types of terrain, since big differences in the rates would account for differences in population density. It was hoped to gain some idea of the distance covered in different kinds of vegetation in a given time and whether there was any consistency in direction travelled. The problem of relative rates was approached by experiments with circular trenches, and by direct observations of the wandering of individuals, which led to experiments on the visual responses of hoppers.

a. Circular trench experiments.

For each experiment a circular trench of about 9 m. inside diameter was dug in a patch of uniform vegetation. The trench was 60–80 cm. deep by 30–40 cm. wide. If hoppers were present in the vicinity a second similar trench was dug outside the first and sometimes vertical partitions of sheet metal fitted in the inner trench, to judge the direction in which hoppers came off the patch. The vegetation patch in the centre was reduced to about 3 m. diameter with an annular space about 3 m. wide. Sometimes a strip 50–100 cm. wide was used instead of the circle of the central patch; it was easier to find hoppers on patches of this shape.

The centre was stocked with a known number of hoppers before sunrise or after dark, and those in the trench were counted at intervals, taking care not to disturb those on the patch. Those in the trench were replaced on the patch in

an unsuccessful attempt to maintain the numbers constant. Early in the experiments counts were made three or four times a day, but it was soon found that at least hourly counts were required. The main difficulty was that birds and animals trapped in the trench devoured the hoppers as they fell in. In fact so many sources of error arose that the experiments were abandoned without giving comparable results.

Trench 1, adjoining millet west-north-west of camp, enclosed a natural strip of *H. pallens* 2.0 × 0.7 m., running east and west. It had been part of a tongue of *H. pallens* continuing into the millet lying east and west of the strip containing an indigenous population of hoppers of all stages. In the week after the trench was dug, few hoppers were found in it daily, but by the end of the week none was found and four in the patch. Of those in the trench, most were in the west sector, some in the north, very few in the south or east.

This patch was stocked with 110 4th instar hoppers after sunset on 15.ii. to test the effect of wind exposure, and boards were put up first as a wind screen. On 16.ii. the trench was examined hourly from 06.40 to 20.20 and a total of 12 hoppers found, on 17.ii., hourly examination gave 10 from 08.00 to 19.00. The boards were removed before sunrise next morning with no apparent disturbance. This day 23 hoppers were in the trench (the day was duller than the two preceding) but only 15 could be found on the patch. This suggested a stimulation of wandering by the wind, but attempts at repetition were abortive.

The patch of trench 2, away from cultivation in zone III, was first weeded and then provided with dead *Suaeda* branches forming a patch the size of that in trench 1. This was to test the effect of vegetation as a mechanical factor in the absence of food, and the effect of wind. At least hourly examinations were made, as before, but the time of stocking was changed to the morning of the experiments, to reduce the ravages of nocturnal predators. One hundred 5th instar hoppers were placed on the branches before sunrise on 27.ii., with a wind screen of matting. Seventy-five came off in the course of the day. Before sunrise on 27.ii. the 56 remaining were removed and 100 added and the wind screen removed. On this day 415 were found in the trench despite fewer examinations which should reduce the total. On both days the weather was similar, which again suggests that windiness stimulates wandering. The *Suaeda* branches and the remaining hoppers were then removed, and at dawn on 5.iii., 100 hoppers placed against the screen. Counts were not frequent enough to compare the totals with the previous days, but without doubt the hoppers, despite the shelter available, left the screen at a greater rate than they had left the windswept branches on 28.ii. This observation, confirmed subsequently in the field, suggested that vegetation, as a mechanical factor, acted as a strong "brake" on movement, or that the absence of vegetation was a powerful stimulant to wandering. This is perhaps connected with the reactions of the hopper to the nature of its substratum, and the poor grip obtainable on the ground stimulates more movement than is made on stems.

Trench 3, with a circle of *H. undulatum* 20 cm. high, was deserted by 71 5th instar hoppers in one day. This is an isolated figure, perhaps of interest in relation to the tendency of older hoppers to abandon *H. undulatum* mats where their earlier stadia were spent.

Parallel experiments were made with trenches 2 and 4. Each had a circle of cut *Panicum* stems 20 cm. high, to simulate dense grass. Bare patches 30 cm. across were interspersed in patch 2 in one day, filled in patch 2 and made in patch 4 the next day. No consistent difference was found in numbers leaving the patch with, and that without, "basking places." The average in a day was

18 in 7 experiments. Comparison of this with previous figures for trench 2 suggests that the much denser vegetation of *Panicum* stems, providing its own shelter, reduced wandering considerably.

Technique could not be perfected in time to give satisfactory results, and it is described to assist others contemplating the use of this method. Similar experiments are mentioned by Johnston (1934). A small patch of vegetation is desirable to check counts made at the end of the experiments, but the diameter of the trench cannot be so small without serious danger of disturbing the hoppers, even if the trench be dug large enough to allow the experimenter to crawl round it out of sight. Counts should be made as nearly half-hourly as possible, and the same number of times daily to give comparable results. If sufficient hoppers be available, it would be better to use a large number, say 500, and not replace hoppers from the trench.

Results of the trench experiments suggest, without proving, that lack of vegetation is a powerful stimulant to wandering, as is wind also, and that more wandering occurred in thinner vegetation. As these results were confirmed subsequently, they may be regarded as supporting evidence.

b. Wandering experiments.

These fall into two sets, those carried on for half-an-hour and those for three consecutive days. In both the main object was to get an idea of the relative rates of wandering in different vegetation zones, but, in the first, an attempt was made to record temperatures and wind strengths along the routes taken by the hoppers.

Half-hour wandering experiments.

Three vegetation zones were used: zone Ib (sand dunes, pl. 2, fig. 3); Ic (pl. 6, fig. 12); and II (dense grass, pl. 3, fig. 5). All three lay near the northern part of the Khor Toqwan cultivation. Always, recently captured, indigenous 5th stage hoppers were used. They were taken daily from the cages and kept in well-aërated tins with food, in the shade, until used. Procedure was as follows: a hopper was carried by hand from the tin to the zone, the experimenter took up an inconspicuous position, crouching or lying on the ground, and threw the hopper 2 or 3 metres from him. Careful placing of the hopper on a grass stem in zone II would have been feasible but was not adopted, so that procedure in all zones might be the same. In zones Ib and Ic careful placing on the ground or thin vegetation was out of the question as subsequent movements of the observer caused the hopper to move away rapidly, or if he remained still, the hopper often climbed on him. It was known already from preliminary experiments that hoppers placed on vegetation tended to remain some time, so that with this method of release no appreciable difference would have appeared in the 3 zones in half an hour, and therefore bare ground away from the nearest bushes was chosen for the starting-place in zones Ib and Ic. Movement was thus ensured and the results made referable to vegetation density. What increase in rate of wandering resulted from this bias in favour of movement may be judged from comparison of the rate in zone Ib in this and in the 3-day experiments. In the latter the average half-hour distance was about one-eighth of the average in the former. This great bias was insufficient to mask the differences in rates on the different zones. A few mechanical devices for releasing the hoppers from a distance were tried without success. The throwing method had the advantage of enabling the hopper to be watched through field glasses. In zone Ib the observer lay behind a mound; in zone Ic, in the shade

of a bush; in zone II the hopper could only be seen for about a metre. This increased the danger of disturbance, but the grass stems screened the observer fairly well, and obvious disturbances were rare. If the hopper approached the observer, he remained motionless until it moved away. When change of position was necessary because the hopper was out of sight it was made with extreme care, and whenever the hopper was disturbed the experiment was discontinued and disregarded.

Notes on behaviour were taken, especially of the situation, the time spent there, and in horizontal movement. On zones Ib and Ic this last meant only movement over bare or sparsely covered ground, since to continue wandering a hopper on a bush had to return to the ground via the base of the plant, and the effective horizontal distance travelled was the main point of interest. At the end of each half-hour's observations, labels were placed on the path taken, and particularly at any point where pause had been made. The temperature (uncoated, unshaded ordinary thermometer) and wind strength ("Wind Speed Indicator," see Appendix) at the points marked was taken immediately. These readings, taken anything up to 35 minutes after the hopper had left the position, gave only the order of difference between the positions. The horizontal distance from label to label was also measured.

Experiments described above were made in each of the 3 zones in turn throughout the day in order to equalise weather conditions.

The quantitative results are summarised in Table IX for zone Ib, X for zone Ic, and XI for zone II. The temperatures and winds are given in the order the points were passed by the hopper, the place where most time was spent being marked in heavy type, and that of a pause of a few seconds in italics. The first figures in each case apply to the condition at starting.

In the dense grass of zone II it was seldom possible to watch a hopper as long as 30 mins. and fewer experiments are worth inclusion.

Considering the distances covered, the figures for zones Ib and Ic are too high to indicate the average distance covered each half-hour in a whole day, but there is a clear correlation between the amount of bare ground and distance covered.

In all 3 zones most time was spent in one place, and only a small part in wandering. In zones Ib and Ic (and also II) the greatest time spent in inactivity was on vegetation, but places where long pauses were not made were neither consistently warmer, cooler, windier, nor calmer than the vegetation where most time was spent. Warmer and better sheltered places could be found on the ground (except in the evening) than those the hoppers found on the plants. It does not appear from the tables, however, that once on a bush, hoppers spent most time in positions better sheltered from the wind and well exposed to the sun. The tendency to continue climbing to near the end of a twig, which may be attributable to negative geotaxis (see under Aggregation, p. 494), accentuated the braking effect of bushes by reducing the chances of random movements carrying hoppers off the bush to bare ground.

These interesting results bear out impressions gained from the trench experiments that the most potent brake on movement in zones such as Ib and Ic is vegetation not as a micro-climatic or food factor, but in a simple mechanical sense.

It is hard to differentiate the influences causing sustained movement on bare ground. Wind, as a mechanical stimulus in conjunction with the poor grip obtainable on the ground, is certainly important. The momentary fluctuations in wind strength appear particularly important, for the hoppers

TABLE IX.

Results of half-hour wandering experiments on hoppers in Zone Ic. Readings at positions where more than five seconds pause made, in italics; readings at positions where most time spent, in heavy type.

Date	Hopper	"Sun temperatures" en route, °C.	Wind strengths en route, m./sec.	Time settled on vegeta- tion (min.)	Time settled on ground (min.)	Total time settled (min.)	Time travel- ling on ground (min.)	Distance travelled (m.)
4.iii.	A	39-38-37-45-40-30-29-28	2-1-2-3-2-2-1-9-3-7-3-3-3-7-2-8	26	1	27	3	18-6
4.iii.	B	38-36-37-39-45-32-30	3-2-4-8-6-5-2-6-0-0-2-8	23½	0	23½	6½	35-7
5.iii.	C	24-25-25-25-25-25	3-6-2-7-1-5-1-5-0-2-5	0	6	6	24	45
5.iii.	B	31-36-37-33-41-32-31	5-2-4-8-1-7-6-9-1-5-0-0	23½	0	23½	6½	16-5
5.iii.	C	35-34-39-33-29-31	3-3-3-5-3-1-6-9-?-2-7	24½	2½	27	3	15-6
5.iii.	D	31-30-29-28-27-29-28-27-29	3-3-3-2-3-0-2-7-3-1-1-7-3-2-2-9-3-6-2-3	3½	0	3½	26½	44-4
5.iii.	E	24-24-24-24-24-24	2-2-2-2-2-2-2-2-3-2-2	0	4	4	26	37
6.iii.	A	26-27-27-30-26-30-41-26	3-7-3-7-3-0-1-5-2-1-1-8-0-2-4	15	2	17	13	36-5
6.iii.	B	30-35-33-20-31	—	22	1½	23½	6½	31-2
6.iii.	C	35-36-30-31	4-8-6-7-3-7-3-0	16	4½	20½	9½	45-7
6.iii.	D	34-30	3-6-1-1	5	15	20	10	31
6.iii.	E	29-27	1-5-0	18	4	22	8	37-4
Means		—	—	14-8	3-4	18-1	11-9	32-9

TABLE X.
Results of half-hour wandering experiments on hoppers in Zone Ib. Further explanation with Table IX.

Date	Hopper	"Sun temperatures" en route, °C.	Wind strengths en route, m./sec.	Time settled on vegetation (min.)	Time settled on ground (min.)	Total time settled (min.)	Time travelling on ground (min.)	Distance travelled (m.)
4.iii.	A	35-34-36-33-31-32-37-32	1.5-1.8-1.2-2.4-1.0-1.7-0.8-0.7	19	4½	23½	6½	14.6
4.iii.	B	36-37-32	2.4-3.1-2.8	28	0	28	2	4.4
4.iii.	C	28-31-33-27-27-30	2.5-1.5-0.6-3.3-3.3-2.1	22	6	28	9.1	9.1
4.iii.	E	27-27-28-26	2.8-3.2-1.5-3.0	25	2½	27½	2½	7.6
5.iii.	A	31-30-27-27-29-29	3.2-3.3-4.4-2.7-2.1-2.0	24	1½	25½	4½	1.3
5.iii.	B	29-32-32-28-27-26	6.7-3.1-6.2-4.2-4.7-4.8	24	0	29	6	8.1
5.iii.	C	38-35-41-34-34-37-38-35	3.3-4.5-3.4-4.8-5.6-4.8-3.5-3.6	6	17	23	7	10.6
5.iii.	D	38-33-31-30-30-32-34	2.9-3.0-2.8-3.1-2.8-2.5-1.8	13	8½	21½	8½	4.8
6.iii.	A	35-41-35-31-27-27	3.0-2.1-2.6-4.2-2.3-1.7	26	1½	27½	2½	8.0
6.iii.	B	—	—	—	—	—	—	12.5
6.iii.	C	—	—	—	—	—	—	9.8
6.iii.	D	—	—	—	—	—	—	19.2
Means		—	—	20.8	4.6	25.4	4.6	9.2

TABLE XI.

Results of half-hour wandering experiments on hoppers in Zone II. Further explanation with Table IX.

Date	Hopper	"Sun temperatures" en route, ° C.	Wind strengths en route, m./sec.	Time settled (min.)	Time travelling (min.)	Total duration (min.)	Actual distance travelled (m.)	Distance corrected for 80 min. (m.)
4.iii.	A	45-42-35-40-32-5	0-0-6-1-8-0-0	23½	6½	30	3-3	3-3
4.iii.	B	42-36	0-8-2-8	29	1	30	0-3	0-3
5.iii.	A	33-32-32-31	2-3-2-6-2-2-1-7	15½	4½	20	1-9	2-5
5.iii.	B	36-33-30	2-2-1-5-3-7	12½	2½	15	1-2	2-4
5.iii.	C	28-29-28	1-5-1-5-0-7	20	3	23	0-9	1-0
5.iii.	D	23-24-24	2-8-1-5-2-3	21	2	23	0-7	0-8
6.iii.	B	34-32	—	18	12	30	6-7	6-7
6.iii.	C	34-31	—	16	4	20	0-9	1-2
6.iii.	D	30-28	—	10	3	13	0-7	1-4
Means		—	—	24-4	5-6	—	—	2-2

were buffeted and unable to brace themselves as against a constant wind. Wind fluctuation is inseparable from body surface temperature fluctuation, although it will be recalled that bare ground was rapidly abandoned in one trench experiment in spite of a wind screen. Hoppers remained long on small sheltered patches of bare ground in cultivation (*see* Aggregation). The difference between such patches and open bare ground outside cultivation, was not only the windiness, coolness and lower humidity of the latter, but also its much higher light intensity. Constant lower temperature is unlikely to be an activating factor, and humidity differences seem also to be not of great importance (*see* p. 480). There was no noticeable correlation between distance covered and time of day in the half-hour wandering experiments in zones Ib and Ic, so the effect of open ground was operative over a great range of temperature and humidity.

On hot days ground temperatures may reach levels avoided by hoppers; it was found that feet were not raised from the ground till surface temperatures approached 50° C. Such high soil temperatures were seldom encountered on wind-swept ground nor were "sun temperatures" over 40° C., and, in cultivation, hoppers remained quiescent on the ground up to, but not above, this temperature. Had temperatures above these been common, the resulting excitement would have accelerated movement on open ground, but they were not found at this season.

As may be seen under Aggregation, inactivity in sheltered places in cultivation, appears connected with close apposition of widely different temperatures and relative constancy in a given place. In zones such as Ib, Ic, and II, the spatial distribution of temperatures was more uniform, *i.e.* the temperature "field" in which hoppers moved was less patchy and temperature in a given place varied because of wind fluctuation. Sometimes hoppers spent some time on the ground in a sunny sheltered spot, especially in the 3-day experiments, but such spots were rare in zones Ib and Ic and absent in zone II.

This is probably the main negative reason for wandering in open zones as compared to sheltered zones, the positive reason being wind and insecurity of foothold. Visual attraction to bushes (*see* below) may temporarily accelerate movement on open ground but the inactivating effect of bushes when reached, makes the net result of visual attraction a reduction of time spent in random wandering.

As stated above distance covered appears unrelated to time of day on zones Ib and Ic, but not entirely in zone II, where, while horizontally the temperature

"field" is fairly uniform, a vertical temperature gradient exists in most places day and night, reversing about sunset and sunrise. The higher temperature in the day is among the grass heads, but at night it is under the grass close to the ground (fig. 14). Hoppers tend to keep near the top of the grass and wander a certain amount in the day, probably because of wind, but about sunset to descend and remain in the same place.

Wind encountered by the hoppers in zone II was weaker than in Ib or Ic, but the slower wandering in II seems due to an easy foothold being available even in the wind. Dense, continuous grass was chosen as it had been deserted by later instars; it must be emphasised that where grass was not continuous but enclosed bare patches, the horizontal temperature "field" was not uniform, and approached the patchy condition of unweeded cultivation. Therefore, the lack of a patchy temperature field and the windiness of open grass, must largely account for hoppers wandering and collecting on the lee edge of the grass or in cultivation, despite the slowness of movement compared to zone I.

That distance covered on zones Ib and Ic was no less in the evening than in the day is due to starting the hoppers on bare ground. In the 3-day experiments they usually remained on the same vegetation from some time during the afternoon, until the end of the experiment at sunset.

No consistency whatever was observed in the directions taken in zone II. On zone Ic a distinct tendency to move into wind not too strong to prevent it (up to c. 6 m./sec.) was found as long as the hoppers were on bare, or almost bare, ground. In small grass and *Panicum* clumps this tendency disappeared. On zone Ib (ground bare except for an occasional bush) the tendency to move into moderate wind was clearly marked, but on zones Ib and Ic it is suggested that sudden change in direction and movement towards some conspicuous object, usually a *Suaeda* or *Panicum* bush, nullified this. Such attraction is strongly suspected in 9 of the 12 experiments in each of the 2 zones. On zone Ic it was not always convincing, but in Ib, where they moved long distances with usually only one bush in view, the apparent attraction was striking, up to 20 m. or more. It appeared unrelated to wind or sun direction and experiments to confirm the attraction were made. There is reason to suppose that the attraction applied to zone II, but distances covered were too small to decide.

The attraction clearly interferes considerably in the generally directing rôle of the wind, and it appears (considering the zones in isolation) that there would be no consistent direction in zone II, a weak tendency to move north in zone Ic, but so counteracted by ground vegetation and attraction to bushes as to be insignificant, and a strong tendency to the north in zone Ib, whilst affected by attraction to bushes, nevertheless producing a real drift northwards.

Three-day wandering experiments.

These were made in an attempt to discover what happened to 5th instar hoppers which strayed into zones where they were not common. Detailed records of time spent in different situations and of micro-climates were not taken. Since many results were desired in a few days, natives were employed to observe 4 hoppers each day. It had been intended to use the same hopper for three days but this was possible only in two cases because of predators and moulting, and hoppers were replaced. The fresh ones were started at the point reached by the predecessor and estimates of distance, etc., presume no replacement. On the first day each hopper was started on bare ground and each evening after sunset it was put in a perforated tin without food and left overnight at the point reached. At sunrise it was released at the same point; at

this time hoppers were inactive and not noticeably excited by handling. Observers were obliged to change position to keep up with hoppers, but this was done carefully and no great disturbance was likely. "Stalking" the hoppers on open ground was not really difficult, especially as all movement was slow, close to the ground, and about 5 m. distant. After each hopper had moved away numbered labels were placed and, at the end of the day, sketch maps were made to show distances and directions of movements.

To retain the hoppers in one zone during an experiment, only zones covering large areas could be used, Ia and Ib, i.e. the open plain and the sand dunes. 9, 10, and 11.iii. were spent on zone Ia between the camp and La'at, and 14, 15, and 16.iii. among the dunes west of the camp. None of the former area contained sufficient ground vegetation to warrant inclusion in zone Ic or III, but sparse recumbent grass and occasional *Corchorus trilocularis* and *Aristolochia bracteata* tufts were present, and hoppers fed on them in their wanderings. A typical condition of the dune *Suaeda* bushes is shown on pl. 2, fig. 2, but they varied considerably. Zone Ib carried on the average larger bushes than on pl. 2, fig. 3, but farther apart and, the dunes being larger, only one bush was visible usually.

TABLE XII.

Results of three-day wandering experiments on hoppers.

Date	Duration (hours)	Hoppers used	Actual distance (m.)	Straight from starting to finishing point		
				Distance (m.)	Direction	
Zone Ia.						
9.iii.	11	A1	315	280	NNW	
9.iii.	10	B1, B2	93	30	NNW	
9.iii.	11	C1	178	146	W	
9.iii.	11	D1, D2	220	186	W	
10.iii.	11½	A1	40	15	NNW	
10.iii.	11	B3	134	118	NW	
10.iii.	11	C2	59	55	N	
10.iii.	10½	D2	148	143	W	
11.iii.	11½	A1	80	67	N	
11.iii.	11½	B3	37	37	NNE	
11.iii.	11½	C2, C3	122	119	NNW	
11.iii.	11	D3	30	24	W	
Zone Ib.						
14.iii.	11	A1, A2	187	101	NE	
14.iii.	10½	B1, B2, B3	201	165	NNE	
14.iii.	10½	C1	27	26	NNW	
14.iii.	10½	D1, D2, D3	227	137	ESE	
15.iii.	11	A2	110	119	W	
15.iii.	11	B3	67	64	E	
15.iii.	10½	C1	110	82	N	
15.iii.	11	D4, D5	7	7	ESE	
16.iii.	11	A2	0	0	—	
16.iii.	10½	B3	0	0	—	
16.iii.	10	C1	134	55	NNE	
16.iii.	10½	D5	7	7	WNW	

The Radio Integrator readings were 40, 44 and 48 c.c. for the 3 days on zone Ia, and 45, 44 and 40 c.c. for zone Ib; although the sun was out less consistently during the experiments on Ia and the screen temperature was on the average higher for Ib than for Ia. The screen humidity was higher for zone Ib, and on 16.iii. there was a little rain.

The daily distance covered by each composite hopper is shown in Table XII, and rough maps of the paths on figs. 7 and 8. These take no account of small meanderings and potterings within a small area. On 16.iii. hoppers were so much less active than on 14 and 15.iii. that the depressing effect of weather is suspect, and results are probably not typical. Nevertheless absence of wandering in Ia seemed inconceivable even in weather as dull as 16.iii. Hopper "E,"

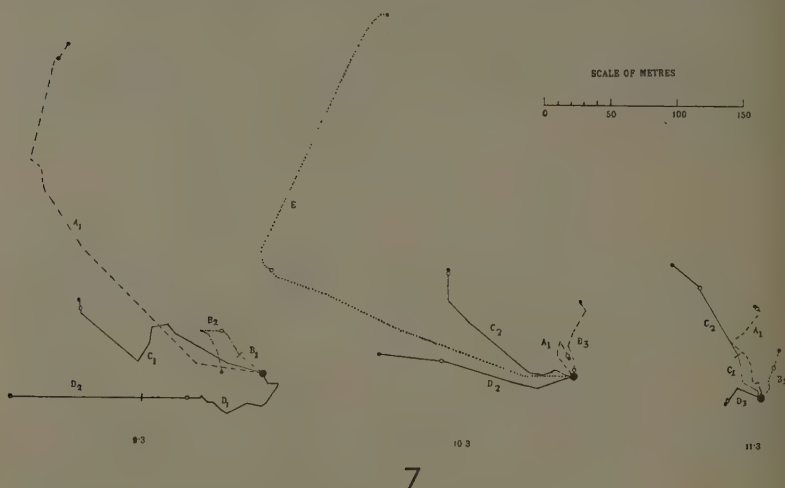


FIG. 7.—Paths taken by 5th instar hoppers on each day in the three-day wandering experiments in zone Ia (pl. 2, fig. 2). For convenience all the hoppers are represented as having been started from the same point on each of the days. Small empty circles indicate the position reached at midday. Transverse lines cutting the paths indicate the point at which a new hopper was started. North at the top of the page.

released with others on 10.iii. on exceptionally bare ground, travelled 448 metres in 10 hours (279 metres as the crow flies). This result is excluded from the averages for zone Ia but "E"'s path is included in fig. 7.

The striking results show that the suggestion that distance covered is proportional to the bare ground present is untenable in this simple form. Even with large expanses of bare ground in Ib the average daily distance was 117 m.² compared with 122 m. in Ia. The average distance in a straight line from start to finish was 87 m.³ on zone Ib as against 102 m. on Ia. The above statement, therefore, must be re-cast as follows: the distance covered on a given zone over a long period was proportional to that separating the vegetation clumps, but

² This omits data obtained on 16.iii., weather very dull; with this included the average was 90 m.

³ 64 m. including 16.iii.

inversely proportional to the size of the clumps. In Ia the clumps were all small but relatively frequent, whereas in Ib they were very large bushes many metres apart. In view of previous conclusions, confirmed in the 3-day experiments, that vegetation acted as a mechanical brake and horizontal wandering was associated with open ground, it was apparent that (independent of the percentage of bare ground) the chances of wandering being initiated depend on a hopper's small random movement on a clump carrying it to the ground. The larger the bush, the longer before the hopper returned to the ground and resumed its horizontal travel. The hoppers moved more rapidly over the bare dunes than over the ground of zone Ia (see half-hour experiments), but once a large bush among the dunes had been reached and climbed, the hopper remained on it longer than on a smaller bush as in zone Ia. This fact was not revealed by the half-hour experiments, but, had they been continued for longer periods, the distance covered on the dunes is likely to have been less than that on Ic

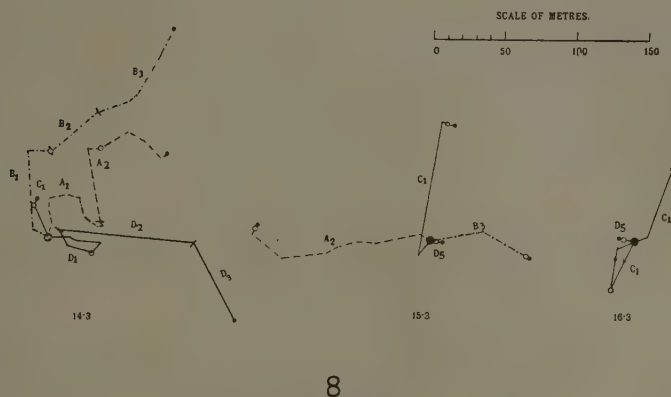


FIG. 8.—Paths taken by 5th instar hoppers on each day in the three-day wandering experiments in zone Ib (pl. 2, fig. 3). Otherwise as fig. 7.

despite better ground vegetation compared to Ia. The greater time spent on large bushes was probably connected with adequate wind shelter available on their lee sides.

The 3-day experiments confirm that most time was spent on vegetation; in fact it was more marked than in the half-hour experiments. Whilst most of the time spent in inactivity was passed on vegetation as before, more inactive time was spent on the ground in the 3-day experiments, particularly in Ia where thin ground vegetation was common. Similarly the tendency for inactivity to be passed in relatively sheltered positions in the sun was more marked than before, although at least one-third of the time of inactivity on vegetation was spent in unsheltered and more or less shaded positions. While it is still clear that periods of activity and inactivity cannot be as well correlated with temperature differences as with other factors, nevertheless more correlation with temperature is evident than in the half-hour experiments.

In zone Ia the effects of high midday temperatures applies as in the half-hour experiments. Soil temperatures over 50°C . or "sun temperatures" of over 40°C . were too rare (owing to wind) to play a large part in activating

hoppers; on the dunes, however, especially on, or at the foot, of the steep lee slopes, they were not uncommon at midday and probably activated hoppers. However, the inability to remain quiescent on open ground was as marked at other times as at midday, and much more time was spent on vegetation than in wandering, so that any slight acceleration of movement on open ground would have a small effect on the net results.

It is interesting that even on flat windless ground in the lee of large dunes, hoppers seldom sat quiescent for long, but potted about within a few square metres, pausing for a few minutes, so that horizontal travel effectively ceased for a period, especially on two occasions. It was striking, also, that when a hopper passed out of the sheltered area into the wind, it accelerated its pace and made a fairly straight course into the wind till reaching a calm place or a bush; furthermore, wandering did not continue at the same rate throughout the day but was usually much more in the morning than in the afternoon. This suggested that the stimulus of release from the tin was felt for some time. On 6 of the total of 24 occasions on the two zones, the greatest distance for the day was traversed within an hour of the start, although it was usually many minutes after the start before the long traverse was made. Otherwise the greatest distance was travelled at various times, but a new, replacement, hopper often made a long traverse. Excitement induced by initial handling seems to have persisted for some time; thus the experiments were less natural than had been hoped and the rate of wandering higher than would be normal. On the other hand, the experiments retain a relative value.

The direction of the hoppers (figs. 7 and 8) again showed a general upwind tendency with a strong westward bias, more marked in Ia where the comparative flatness allowed the tendency fuller play than in Ib or Ic. The large bushes

TABLE XIII.

Results of three-day wandering experiments on hoppers expressed in terms of four hoppers in each zone.

“ Hopper ”	No. of hoppers used	Straight from starting to finishing point		Actual distance (m.) Y	Approx. ratio, Y/X
		Direction	Distance (m.) X		
Zone Ia.					
A	1	NNW	310	440	1.4
B	3	N	120	190	1.6
C	3	NW	340	430	1.3
D	3	W	350	400	1.1
Means	—	—	280	365	1.4
Zone Ib.					
A	2	NNW	90	300	3.3
B	3	NE	200	270	1.4
C	1	N	160	270	1.7
D	5	ESE	140	240	1.7
Means	—	—	147	270	2.0

attracting the hoppers and steep lee slopes of the dunes caused frequent deviations in Ib. The difference in consistency of direction in the two zones is emphasised in Table XIII, where movements on one zone under symbol "A" are treated as though made by one hopper for 3 consecutive days, and the same has been done with "B," "C," and "D." The figures have an indirect bearing on what one hopper would "naturally" do for 3 consecutive days (it would probably be taken by a predator during this time), but only the relation between the two figures can be considered seriously. The ratio of distance travelled to that covered in a straight line is larger on the dunes than the open plain, reflecting the stronger deviating influences of the dunes; moreover, in Ia the points reached all lay, in relation to the starting-point, in the north-west quadrant, whereas on the dunes the directions are more fanned out. In zone Ia the general north-west direction was away from the sun and into the wind as more movement took place in the morning. It is suggested that both factors play a part. Insufficient long traverses after midday are available to judge the favoured direction at this time.

Table XIII and figs. 7 and 8 show that even on zone Ia the north-west tendency is far from invariable, and in no zone can hoppers be imagined moving rapidly in one direction so as to be trapped in another zone to the windward.

In these experiments, as in the half-hour ones, the impression that hoppers were attracted to bushes irrespective of direction was strong. With the many occasions when the attraction was anticipated but did not occur, was a substantial minority when it did occur.

c. Visual attraction experiments.

The impression that hoppers were visually attracted to conspicuous vegetation was potentially so significant that methods of verification were tried.

The first was to drive them out of vegetation for short distances, at first on a mat of *H. undulatum* (pl. 3, fig. 4). Most of the hoppers were 2nd-4th stage and, by walking through, hoppers were driven out on the bare sand. When they were a metre or two from the edge of the mat the observer sat on the ground and remained motionless; the great majority turned in a few seconds and returned to the mat, irrespective of the direction in which it lay. They were driven out in all directions and always returned. It was clear that wind, sun, or smell could have nothing to do with it. This was repeated with similar results on small isolated patches of millet among the dunes where older hoppers were present.

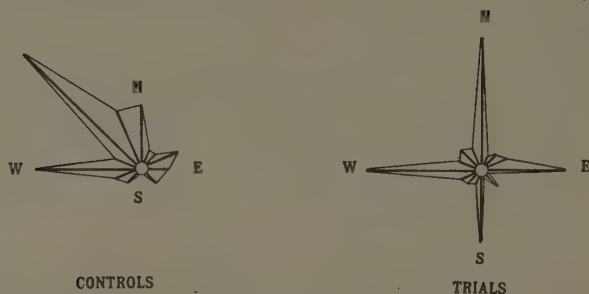
The second method was to release hoppers near a large bush standing alone among the dunes. The hoppers went to the bush in rather less than half the cases irrespective of wind or sun. The less positive results in this case may well be due to great excitement resulting from handling.

In the third method an attempt was made to achieve better controlled conditions, to reduce excitement, and conceal the experimenter entirely. True indigenous hoppers were not available and *dissocians* was used. Only pure green-coloured extreme 5th instar hoppers were selected, from a place where they were known not to have been in band formation since the 1st instar.

Experimental method.

Conditions were arranged to give the optimum opportunity for any latent force of visual attraction to appear. The arrangements are shown in pl. 9, fig. 17. A pit large enough to hold a man was dug in the middle of the large completely flat, bare area north of the camp, and covered with a circular matting

90 cm. in diameter, supported by sticks and fastened firmly at its edges. The 8 principal points of the compass were marked on the ground, and circles concentric with the matting were marked outside it at regular intervals. A sprig of *Suaeda* projected about 7 cm. from the middle of the matting, and half of a *Suaeda* bush nailed to the front of a box 1.5 m. from the centre of the matting presented a frontal area about 1 m. square and subtended an angle of about 33° . The observer, behind the box, was invisible from the matting and noted the behaviour of the hoppers through a small hole in the box, as they left the sprig. The assistant in the pit placed a hopper low on the sprig and it climbed through the hole in the mat. Usually it paused some seconds, sometimes minutes, near the top of the sprig, climbed down and wandered off the mat. After climbing the attached bush or wandering 10–15 metres it was captured and placed in a separate cage behind the box. A fresh hopper was used each



9

FIG. 9.—Experiments on visual attraction to vegetation. Directions from the centre of the matting of points at which hoppers first crossed the 1.5-m. circle. Length of each radiating line proportional to the percentage of individuals crossing at the direction concerned, out of a total of 46 control cases with no conspicuous object, and 96 trial cases with the bush placed N, E, S and W on an (approximately) equal number of occasions (Table XV).

time, the procedure being to set the box with the bush at each of the cardinal points of the compass an equal number of times in one set of experiments. Four hoppers were used with the box in each position and each made to climb a different side of the sprig.

In the control experiments without the bush, was a second uncovered pit, 6 metres south of the main one, with an observer in it. When on or near the matting a hopper was observed by periscope, but when farther away the observer had to raise his head, although this appears to have had no effect on the subsequent path.

Because of the intolerable conditions in the pit experiments could only be made in the early morning or late afternoon. Readings of wind direction and strength near the ground (airmeter spindle 5 cm. off the ground); sun direction; light intensity (without the bush) by an Exposure Meter (*see* Appendix) north-, south-, east-, and westwards; and "sun temperatures" on the ground were taken. The bush reduced the reading of the Exposure Meter, when placed on the centre of the mat and directed horizontally, by about one-half.

Results.

The conditions and results in the trials and controls are given in Tables XIV, XV, and XVI, and fig. 9 illustrates diagrammatically Table XIV. All results are treated together despite differences in conditions. For analysis only those

TABLE XIV.

Conditions and results of experiments on visual attraction of hoppers to vegetation.
 "x" denotes illumination intensity below 20-30 metre-candles.

Date	Controls.			Trials.			
	3.iv.	4.iv.	6.iv.	29.III.	30.III.	4.iv.	6.iv.
Duration	06-45-08-30	05-40-07-00	05-50-07-30	06-45-10-00	06-15-09-15	17-05-17-45	07-30-08-40
Sun temps. on ground, °C.	27.8-32.0	24.5-37.0	26.0-28.0	26.3-38.0	24.8-36.5	30.5-29.0	28.0-31.8
Sun direction	ESE	E	E	ESE-SE	E-ESE	W	ESE
Light intensity (metre-candles):							
N	930-3880	540-1850	650-1400	—	—	650-x	1725-7000
E	1675-sun	2450-sun	1300-6150	—	—	760-x	1400-sun
S	1100-3800	540-2050	880-1500	—	—	760-x	1830-6130
W	970-3325	540-2050	650-1825	—	—	sun-x	1830-7000
Wind direction	N	NW	N	N	NNW	NE	N
Wind 5 cm. off ground, m./sec.	2.6-3.3	0-1.3	1.9-2.9	3.0-4.8	3.1-3.1	3.0-2.2	2.9-4.2
Hopper directions:							
N	2	3	0	5	7	6	5
NNW	4	1	0	0	2	0	1
NW	5	6	3	2	2	0	0
WNW	0	2	0	0	1	0	2
W	1	2	6	6	9	3	3
WSW	2	0	0	3	0	0	0
SW	0	1	0	0	1	0	1
SSW	0	0	0	1	0	0	0
S	0	0	0	5	3	2	1
SSE	0	0	0	0	0	0	0
SE	0	0	1	3	0	0	0
ESE	0	0	0	0	0	0	0
E	0	0	2	5	5	1	3
ENE	1	0	2	2	1	1	0
NE	0	0	1	0	1	2	0
NNE	0	0	1	0	0	1	0
Totals	15	15	16	32	32	16	16

occasions (50) when the hopper reached the box at the moment of its *first* crossing the 1.5 m. circle are considered "successes" although this makes the proportion of successes appear less striking than it was. Cases where the hopper wandered outside the circle and then turned to the box were, to make the results of the controls and trials comparable, not regarded as "successes." The "directions" in Table XIV are, then, those of point of first impact on the 1.5 m. circle from its centre, and not necessarily those in which the hoppers were going when they reached the bush or other point on the circle.

Table XV shows that in the controls north-west was the most favoured direction, but in the trials in which the bush was used the four directions in which it lay were most favoured. As was expected from the results of the controls, more hoppers still went north or west than south or east, but instead of north-west most went north or west where the bush was, while the number going south and east was much greater than in the controls. When the control and trial distributions in quadrants were compared statistically, the value of χ^2 (Fisher, 1936) was 8.89, indicating that the odds against the differences between the two distributions being merely due to chance were between 20 to 1 and 50 to 1. The use of quadrant distribution disregards the fact that in the controls 14 (of 46) went north-west, while in the trials only 4 (of 96) did so, and this is doubtless significant.

TABLE XV.

Combined results of experiments on visual attraction of hoppers to vegetation.

Hopper directions	Controls		Trials	
	Totals	Totals in quadrants	Totals	Totals in quadrants
N	5	18.5	23	30.5
NNW	5	—	3	—
NW	14	—	4	—
WNW	2	—	3	—
W	9	20.5	20	29.0
WSW	2	—	3	—
SW	1	—	2	—
SSW	0	—	1	—
S	0	1.0	12	15.5
SSE	0	—	0	—
SE	1	—	3	—
ESE	0	—	0	—
E	2	6.0	14	21.0
ENE	3	—	4	—
NE	1	—	3	—
NNE	1	—	1	—
Total	46	46.0	96	96.0

TABLE XVI.

Proportion of occasions on which hoppers reached the bush in experiments on visual attraction.

Date.	29.iii.	30.iii.	4.iv.	6.iv.	Totals
Bush position :					
N	3	6	3	4	16
W	5	6	2	2	15
S	5	3	2	0	10
E	3	3	1	2	9
Total "successes"	16	18	8	8	50
Total trials	32	32	16	16	96

Table XVI shows that hoppers reached the bush at the moment they first crossed the 1.5 m. circle in rather more than half of the 96 cases.

A set of trials with the box at 3.4 m. instead of 1.5 m. was made on 1.iv. The bush was reached on first impact on the 3.4-m. circle in only 7 of 32 cases (9 including those in which it was finally reached).

Operative distance of attraction.

For purposes of analysis the distance over which an attractive force was assumed to operate was only 1.5 m., but in fact hoppers often came to the box from greater distances; in these cases the hopper usually wandered in some direction other than that of the bush, perhaps meandered, and changed its direction suddenly as if becoming "aware" of the bush, and turned straight to it, usually at an accelerated pace. In the 62 cases where the hopper at last

reached the bush at 1.5 m. the frequency distribution of distances over which they went straight to it was: up to 2 m. in 50 cases; between 2 and 3 m. in 6; between 3 and 4 m. in 3; 4 and 5 m. none; 5 and 6 m. in 2; 6 and 7 m. in 1. In the 3-day wandering experiments on the dunes (see above), attraction to large bushes over distances greater than 7 m. was suspected.

Effects of sun and wind.

Factors influencing the direction of movement in the absence of influence from a conspicuous object are of great interest.

The tendency of hoppers to move upwind was noticed in all observations on their movements. If wind strength just above ground exceeded 6 m./sec. they were unable to move directly upwind but frequently re-orientated themselves facing into the wind whenever they paused, and moving in this direction were blown out of their upwind course once more. However, if the wind were the only directing influence, the number on either side of the wind line should be about equal in a number of results.

This was not so. In the controls a marked bias to the west was noticed. In each set of experiments the directions were divided into those within 90° each side of the upwind direction and those beyond 90°, that is, more or less downwind. Cases on the dividing line were assigned equally between the two. In three sets of controls (46 cases) 37 fell in the first, "generally upwind," and 9 the second, "generally downwind" category. The sun was in direction between 90° and 135° to the wind direction. The hoppers' directions were then divided into those on the same side of the wind line as the sun, and those on the side away from the sun, the border line cases being again equally apportioned. In the 3 sets of controls, 14 fell on the sunny side and 32 on the other.

Many preliminary experiments were made before the above technique was evolved. The circumstances differed from those described in a number of ways and results are not comparable as regards attraction to objects, but similar effects of sun and wind direction were noticed and it seems worth including all figures obtained where hoppers did not go to the object. I am convinced that I could distinguish whether a hopper was affected by the object; not only its direction but its manner of movement changed and it either reacted and came straight to the object or wandered off "ignoring" it. If this is even partly true one may analyse the results of all trials where the hoppers did not come to the object, as was done for the controls.

This analysis, with that of the controls, is in Table XVII and it may be seen that in 177 cases, direction was "generally upwind" in 126.5, and "generally downwind" in 50.5 cases. Of 169 cases hoppers deviated away from the sun in 118.5 and towards the sun in 50.5 cases. The 8 cases in the trials on 4.iv. are omitted in the analysis of the sun's effect, as they occurred after sunset when light intensity was much lower. The reactions of locusts to light is discussed more fully under Aggregation, but it may be noted that there is good evidence of positive phototaxis at low light intensities, which may reverse to negative or disappear at high intensities, but in this case the evidence is not conclusive. Results of the above experiments support the idea of negative phototaxis at high intensity.

It is difficult to be sure that a given factor is isolated in the field and there is doubt whether the bias to the west may be due not to the sun's position in the eastern sky, but to sources of attraction in the west. Vegetation to the west of the pit was not appreciably more conspicuous than that in other directions, and the maximum angle subtended by the distant vegetation from the centre of

TABLE XVII.

Analysis of relation of sun and wind direction to direction of hopper movement on bare ground.

Date	22.iii.	24.iii.	25.iii.	26.iii.	29.iii.	30.iii.	1.iv.	3.iv.	4.iv.	4.iv.	6.iv.	6.iv.	Totals
Wind direction . . .	E	NNE	N	NNW	N	NNW	NNW	N	NW	NE	N	N	—
Sun direction . . .	S *	ESE	SE	ESE	ESE	ESE	ESE	ESE	E	W	E	ESE	—
No. up to 90° each side of wind direction . . .	24	4	14	10	5.5	9	14	12.5	14.5	7	10	2	126.5
No. up to 90° each side of direction opposite wind . . .	0	14	8	0	5.5	4	8	2.5	0.5	1	6	1	50.5
No. deviating from wind-line to sun side . . .	9.5	0.5	5	3	6	4	7.5	2	7	(6)	5	1	50.5
No. deviating from wind-line to side opposite sun . . .	14.5	17.5	17	7	5	9	14.5	13	8	(2)	11	2	118.5
Total . . .	24	18	22	10	11	13	22	15	15	8	16	3	177

* Overhead.

the matting was no more than 2-3°. Moreover, the western bias in the morning was also seen in the 3-day experiments, when each hopper had a different visual field. It is hoped that these, and other experiments described here, may be repeated in the laboratory.

Nature of the attraction to objects.

In considering the applicability of results to Concentration and the nature of the reactions, certain peculiarities must be borne in mind. In all observations of visual attraction to vegetation, hoppers were, in varying degree, excited. In the wandering experiments this was engendered by the wind, etc., in the preliminary field experiments on field attraction by driving or handling them, and in the visual attraction experiments proper again it was due to handling (although somewhat "damped" on the *Suaeda* sprig). The first reaction of a disturbed hopper was to make for the nearest conspicuous object. Striking observations of this were made on the bare ground near the site of the visual attraction experiments. When a hopper wandered from the matting, it hopped wildly away when the experimenter approached to retrieve it, but if he kept still, a metre or so from it, its first excitement died and it continued more slowly or even paused; if now the observer kept his legs and body quite still and moved his hands towards the hopper it again moved rapidly, but often turned straight to his feet and climbed on them. This was despite the fact that the source of disturbance (hands) had originally been between the hopper and the source of attraction (legs). In the wandering experiments where excitement was least, attraction to bushes was observed less often than expected from other observations.

Secondly, in the visual attraction experiments proper, hoppers issued from a dark pit into brilliant sunshine and may have been in a state of comparative dark-adaptation.

If it is correctly concluded that in moving from the sun hoppers showed negative phototaxis under the described conditions, the simplest explanation

of the attraction to the bush is also negative phototaxis, but, at low light intensities and the generally unexcited condition of laboratory experiments, Acridids in general (including *S. gregaria*) are positively phototactic, and yet in the field and the trials on 4.iv. visual attraction to bushes (always darker than their surroundings) was present even after sunset with light intensity similar to that of the laboratory. It is thus very difficult to regard this as simply negative phototaxis.

The probable explanation is that the reaction is different from simple negative phototaxis, associated with objects of particular form and brightness, and superimposed on the simpler types of visual reaction according to degree of excitation and perhaps other factors. The peculiar behaviour in the experiments recalls examples of "Formensehen" (Weyrauch, 1936; Buddenbrock, 1937) or "Skototaxis" (Alverdes, 1930; Dietrich, 1931; Klein, 1934; Buddenbrock, 1937), in which a special attraction supervenes over simpler reactions to light.

Discussion of results.

Although visual attraction to vegetation as an aid to concentration or even its existence in phase *solitaria* is not mentioned in the literature, nevertheless it may often have played a part in movements ascribed to other factors. It has, however, been specifically cited in connection with behaviour of marching bands of *S. gregaria*, particularly in the evening (Fraenkel, 1929; Williams, 1933). Zimin (1931) notes the attraction of *Calliptamus italicus* L., hoppers to bushes, particularly of light-coloured plants illuminated by the setting sun, but it is uncertain that such bushes, seen from the ground, would appear darker than the sky. Predtechensky (1935) described *S. gregaria* hoppers returning immediately to bushes from which they had been driven at midday; this appears certainly due to a visual response. Fraenkel (1929) suggested negative phototaxis as the reason for attraction to dark conspicuous bushes in the evening. Lépiney (1933) doubted this as the bushes are often better lit than the soil surface; the point, however, is rather the relative illumination of the bushes and the sky behind, than of the bushes and the ground. Nevertheless, visual attraction to bushes is probably not simple negative phototaxis.

The observations on the effect of wind and sun on the direction of wandering by solitary hoppers have also no close parallel in the literature and it is not obvious what light they can throw on the direction of marching bands. The only case agreeing with my results is mentioned by Predtechensky (1935). He observed that newly hatched gregarious hoppers of *S. gregaria* moved away from the sun, but a number of authors have described occasions when directions were without relation to known external factors (Lépiney, 1931; Williams, 1933; and Predtechensky, 1935, *S. gregaria*; Smee, 1936, *Nomadacris septemfasciata* Serv.; Sviridenko, 1924, *Dociostaurus maroccanus* Thnb.). A band observed by Williams completed $2\frac{1}{2}$ circles with many off-shoots in one day.

Lépiney (1931) and Fraenkel (1929, 1932) record that bands scattered over a large area may follow independently the same direction with no obvious controlling agency. This was very marked at Hamashiameb. When marching began the bands moved northwards almost without exception over the whole area, and this continued morning and afternoon for 3 days. Direction was partly influenced by vegetation and relief and bands wended their way along lanes of bare ground between weeds and mounds. Afterwards the direction changed completely to south-south-west towards the distant hills; this general

direction continued till all hoppers were 5th stage despite repeated disturbance and destruction by control squads.

Lépiney thinks (1931) that mode of wandering may be of two kinds: that with no common direction or persistence, and that of concerted marching in one direction. He considered the dominant form to be dependent on seasonal weather variations, but Lépiney and Fraenkel (1932) agree that while factors controlling the direction taken by a band seem external, there is no evidence of their nature.

A tendency to persistent movement downwind is mentioned by Fraenkel (1929 *S. gregaria*), Cotterell (1930 *L. migratoria migratorioides*) and Moritz (1914 *Calliptamus italicus*, quoted by Zimin, 1931), in contradiction to my observations on solitary *S. gregaria*. My observations contradict also those of Köhler (1937), Gonzales (1932 *L. migratoria manilensis*) and Moritz (*loc. cit.*) on movement towards the sun. Zimin (1931 *C. italicus*, 1934 *C. turanicus*) gave a convincing description of apparent "menotaxis" (Kühn, 1919; Fraenkel, 1931) where hoppers kept their left side to the sun throughout the day's wanderings, moving south in the morning, south-west, west, and north-west in the day and north in the evening. Since precise orientation to the sun's rays is well known in quiescent locust behaviour (Fraenkel, 1930); menotactic responses to the sun are known (Fraenkel, 1931; Buddenbrock, 1937); and the various and apparently contradictory observations on angle of orientation to the sun might be reconciled if the angle be assumed to be variable (Fraenkel, 1931), it does not seem wise to disregard Zimin's observations, which may be the key to the problem.

Further investigation must be awaited before the solution of the problem of marching direction. Meanwhile it is interesting that many authors, including Zimin, mention that relief and vegetation may mask consistency of direction even in gregarious bands, so that it is not surprising that the directions of solitary hoppers lacked consistency in zones such as Ic or II.

As concerns concentration the significance of visual attraction to vegetation is less obscure. The success of the experiments on visual attraction caused the question of hopper movement and concentration to be seen in a new light. Over distances up to say 10 m., visual attraction appears an efficient means of gathering into concentration zones, for these were characterised by their higher and more conspicuous vegetation (pl. 6, fig. 12). Perhaps even more important is its efficiency in preventing hoppers from leaving the zones when once entered. By these means concentration zones presumably act in a literal sense as traps.

(v) Notes on movements and concentration in relation to micro-climates.

1. The two features of natural environments most often correlated with Acridid distribution are plant associations and micro-climates. These are considered interdependent, but Zolotarevsky (1937) has urged that the effects of vegetation as food can be separated from those of its density and micro-climates. So far as plants act as indicators of hopper abundance it is concluded above that it is not primarily because of their food value. Relative density of vegetation, irrespective of the species, appears of primary importance (Uvarov, 1928). Often a statement regarding a plant association carries an implied statement of the horizontal and vertical density of the vegetation, but this was not the case at Hamashameb.

2. The study of micro-climates seems a more promising line of approach. Golding (1934b) said of certain ACRIDIDAE "... their choice of stations

appears to be influenced by micro-climatic conditions." This view is widely held.

3. Correlation between Acridid distribution and micro-climates may be found. In relation to vital processes (development, sexual maturation, longevity, etc.) micro-climate is clearly of importance (Bodenheimer, 1930; Hamilton, 1936) and is, in the end, a limiting factor. A comparative study of a few micro-climatic elements has shown some correlation (*e.g.* Smee, 1937) with the biological processes in the insects which were present and remained in the zones compared, but it is doubtful whether an investigation of that type would lead very far. As Golding says (*loc. cit.*) the study of micro-climates "presents more difficulties than any other branch of our work."

At Hamashiameb, where a few recording instruments were available, attempt was made to obtain comparable records of conditions in different zones, but they are not incorporated in this paper because technical difficulties in maintaining instruments with moving parts in a dust- and sand-laden atmosphere, and lack of time for checking, vitiated the results.

4. The main concern of the investigation being the causes of distribution within an area such as Hamashiameb, the controlling factors cannot be taken as those most affecting the vital processes of insects assumed to remain in one place, such as an air-conditioned breeding cage. With active insects such as locusts the controlling factors must be regarded as those most affecting behaviour and horizontal movement, for the point is not what may be the limiting factors in the last analysis but the *operative* limiting factors for animals which cannot be assumed to remain in one place.

5. Perhaps because of their undoubted importance in vital processes, temperature and humidity are usually the factors first considered in a study of micro-climate.

6. It is sometimes forgotten that stimuli like temperature and humidity (and olfactory stimuli, Trägårdh, 1913) can operate only through the *kinetic* and not the *tactic* reactions (tropisms) of the insect. Vinokurov and Rubtsov (1930) believe that the explanation of rate and direction of movement in Siberian ACRIDIDAE must be sought in meteorological factors: "The movement of ACRIDIDAE from higher to lower ground during drought, or in the reverse direction during wet weather, is due to thermo- and hydrotropisms." Possibly movements from one area to another are due to differences of temperature and humidity, but it is another matter to apply the term tropism, implying that they are directed by these stimuli. Even were one to agree with Zakharov (1932) in regarding all movement as a purposeful attempt to reach an optimum, one cannot escape the question of "how a locust in a certain humidity in one place can know in what direction to go in order to approach a more suitable humidity" (Micheltmore, 1934). Micheltmore was referring to movement of flying swarms on a large scale, but his remark applies to a small scale equally. Supposing each zone completely uniform, temperature and humidity gradients would be, except at the line of contact of two zones, so gentle as to be negligible, and "in all but the most uniform country local humidity gradients are superimposed upon and mask the general original one" (Micheltmore, 1934). Therefore, directed reactions ("tropisms" or taxes, see Appendix 3) to temperature and humidity cannot be considered helpful in directing movements of Acridids towards concentration zones (compare Fraenkel, 1932, on flight direction of swarms).

7. The nature of behaviour and amount of wandering will depend on the presence or absence of differences within a zone. Local gradients will deter-

mine distribution as well as activity levels. The study of micro-climates is much more difficult in relation to behaviour than to vital processes, for, as Uvarov (1928) states, before starting their study a thorough knowledge of the situations in which the hoppers spend their time is necessary. The data obtained from a few thermographs and hygrographs placed in random positions bear so little relation to the kaleidoscopic conditions experienced by active hoppers that they are more trouble than they are worth.

Maxwell-Darling (1936, Tables III and IV) gave figures of air temperature and humidity inside green millet and outside on a bare dune. The differences are small and permit no conclusions to be drawn. His Table V and my Table IX show how the results of a comparison of two zones is altered according to the positions for taking readings. In millet locusts spend most time on the ground but in the dunes most is spent on bushes, so that comparison of two places at equal heights would not reveal the true nature of the difference in conditions experienced by the locusts. Zolotarevsky (1933, *L. migratoria capito* and 1936, *S. gregaria*), Golding (1934) and Lean (1936, *L. migratoria migratorioides*) give figures for air temperature and relative humidity for zones with differing population densities, but the connection between the figures and presence or absence of locusts remains obscure.

Differences in micro-climatic "pattern" or "field" are of more interest for behaviour than any differences between single places or between averages for a number of places. By micro-climatic field is meant the spatial lay-out of each micro-climatic factor: e.g. not only what are the temperatures throughout the day, but what are the differences and how steep are the gradients. To obtain sufficient quantitative data on movements and micro-climates a most elaborate system of micro-climatic "mapping" would be necessary.

Only within the concentration zones were the locusts common enough to provide a good picture of behaviour to which multiple micro-climatic observations could be related; these are described under Aggregation. Temperature apparently assists in reducing range of movement within the concentration zones, not by being generally higher but by its great "patchiness" contrasted with its comparative uniformity on more open ground.

8. Such components of micro-climate as wind and light must be included in micro-climatic maps and most investigators are ill equipped to study these factors. My investigations suggest that wind, for instance, plays a more important rôle in movements in some non-concentration zones than do temperature and humidity.

9. The opinion that the real ecological "meaning" of differences in vegetation character and density lies in the dependent differences in micro-climates, can only be accepted with important reservations. The most elaborate study of temperature, humidity, wind and general light intensities would disregard certain key factors in concentration, which fall outside any ordinary definition of micro-climate, among them visual attraction to vegetation, the mechanical "braking" effect of undergrowth and secondary effects of vegetation sparsity such as exposure to disturbance and predators.

10. To sum up, the study of the relation of micro-climates to movements and concentration is a task requiring more attention to factors other than temperature and humidity than has been usual, and especially to the "pattern" in which each factor is laid out. It is of such magnitude that until a full preliminary study of behaviour has been made, the attempt is hardly worth undertaking. Furthermore, emphasis on the purely micro-climatic aspect of a zone may be misleading.

(vi) *Discussion and conclusions on hopper concentration.*

From observation of hopper distribution and movements there is no evidence that they can be directly attracted from such distances as 100 metres to the concentration zones. Micro-climatic differences would in no way assist in directing hoppers to such zones.

Since this is so, good conditions for concentration would obtain if there existed the maximum possible difference between the zones concerned in the rate of random wandering. If wandering rapidly in all directions occurred in non-concentration zones but ceased in concentration zones the prospects of concentration would be excellent. How far short of this ideal the actual conditions fell, is now considered.

Unfortunately wandering experiments were only feasible in few zones where hoppers were never common. From the above observations something is known of the behaviour of older hoppers on the barest zone (Ia, b, and c) and from those described later under Aggregation something is known of behaviour in zones of densest vegetation constituting the concentration zones. One may guess at behaviour in zones of intermediate vegetation density such as III by interpolation between the two extremes.

The average daily travel on zone Ia was high (122 m.) and was attributed to the activating influence of wind, the infrequent application of the "brake" of vegetation, the inefficiency of this when applied (*i.e.* small size of bushes), the comparative uniformity of the temperature "pattern," and perhaps the high light intensity. The paths taken were comparatively straight; the ratio of distance travelled to that direct from start to finish was small. This was attributed to absence of large vegetation clumps or steep slopes likely to cause deviations and the relatively uniform visual field. Moreover the hoppers' paths usually lay upwind and away from the morning sun. North to north-east wind being general, the hoppers travelled west-north-west to north-west; it is uncertain whether the normal direction would also be away from the afternoon sun; if so the resultant direction would be north, and the ratio of distance travelled to that from start to finish would be larger than in the experiments.

Assuming the afternoon decrease in wandering to be a real phenomenon, as suggested by subsequent observation, it is clear that the movement described cannot usually contribute to concentration. Where a concentration zone happened to lie to the north-west a good proportion of hoppers would reach it, but if it lay in any other direction few could be expected to do so. The advantage of rapid wandering is thus largely nullified by the wandering not being random in direction.

In zone Ib the rate is probably less than in Ia; it is governed by similar factors to Ia, but comparative wind shelter which is common acts as a secondary brake on movement. Wandering seems more consistently directed than on zone Ic, but owing to deviations caused by relief and visual attraction, less than in Ia. Zone Ib, with a high wandering rate (daily average 117 metres) and a fair degree of randomness is probably of all non-concentration zones the one from which a neighbouring concentration zone is most readily reached.

In Ic the wandering rate is certainly lower than in Ia, but whether lower than in Ib is doubtful despite the results of the half-hour wandering experiments. The factors governing wandering are probably similar to Ia, the lower rate being due to the braking effect of the better vegetation cover. Directions were intermediate in consistency between Ia and Ic and movements not random enough to ensure equal chances of reaching concentration zones on all sides.

In better covered zones such as II or III, wandering lost all trace of consistent direction but the advantage of randomness was lost by further reduction in rate.

In zone II the braking effect of undergrowth is at a maximum and movement is slow, but it seems reasonable to suppose the rate of horizontal movement to be higher than in unweeded millet. During the day hoppers tend to be at the top of the grass (unless the wind is very strong), probably because the temperature is usually higher. Here they are buffeted by wind and the horizontal temperature pattern is almost uniform, so there is nothing to interfere with any tendency to slow movement. A clear case of concentration being aided by micro-climatic differences was the collection of hoppers in bare patches in the grass.

No direct observation on wandering in zone III was possible, but some idea may be formed. The low irregular nature of the vegetation made its braking effect almost as strong as in II and quite as strong as in the concentration zones. Temperature and humidity pattern is patchier than in I and II, so that local gradients influence behaviour, since basking was observed frequently. Wind shelter is frequent. The rate of wandering must therefore be lower than in the above zones. Whether the temperature field is more uniform than in concentration zones is difficult to determine, but wind shelter is much less continuous vertically or horizontally, so that the wandering rate in III is probably higher than in the concentration zones, perhaps of the order of 3 m. per day. Doubtless the directions of wandering in this zone are almost entirely random, compensating somewhat, in assisting concentration from all directions, for the slowness of wandering.

The conclusion that the factor of differential wandering rates can only contribute to concentration of older hoppers over short distances, say up to 50 m. (assuming fixed margins to the zones), emerges from the above considerations and observations in the field. Where the rate is high, concentration chances are largely vitiated by tendency to wander in one direction, only exceptionally towards a concentration zone. Where direction is random, the rate is low.

Differential wandering rates account for many aspects of distribution, but as they cannot assist concentration except over short distances, the great importance of visual attraction, also operative over short distances, is apparent.

Sometimes visual attraction retards concentration. On the dunes, for instance, it draws the hoppers from the activating open ground to large bushes where they are long delayed. Nevertheless, visual attraction must have more positive aspects than any other single factor in concentration, for several reasons. Firstly, it tends to prevent wandering away from a cultivated area, for where a better covered zone is separated from a less well covered one by a sharp margin (a frequent occurrence) they will tend to keep in the former and so to the immediate vicinity of cultivation. Secondly, vegetation of a concentration zone stands out most conspicuously from its surroundings so that visual attraction to it would be most powerful. Thirdly, and perhaps most important, it converts concentration zones into effective traps. The lower wandering rate in millet tends to trap hoppers, but the possibility of wandering out again is not excluded. In practice those wandering or driven from a concentration zone are virtually forced to return, as disturbance or impact of wind will excite them. Visual attraction must therefore increase many times the efficiency of concentration zones as traps.

The emphasis on the rôle of visual attraction must not obscure the fact that with no initial tendency to wander Real Concentration would be impossible.

Concentration from IVb (weedless millet) into IVc (millet with weeds) is the one important case where visual attraction cannot add to the effects of differential wandering rates. There is probably no appreciable visual discrimination between weeded and unweeded millet, and the lack of braking effect of ground vegetation in weeded millet is probably an important factor.

Conclusions on the changes in hopper distribution (Table VII, p. 412), and resultant concentration, may now be suggested.

Young hoppers of the 1st winter generation hatched all along the course of the flood, particularly where millet was grown the previous year, but in varying degree in all types of the current season's zones, and up to 100-150 m. from the dune margins where most millet was planted. Those hatching on bare ground (many, especially along the marginal dunes) must have scattered till they encountered edible vegetation, usually *H. undulatum* mats on the dunes, elsewhere *H. pallens* and grasses. Even in millet wandering appeared to continue till weeds were met. The evidence suggests that young hoppers ceased wandering after their first meeting with good ground vegetation.

As they aged their numbers decreased but their mobility increased. Older hoppers, especially 4th and 5th instars, tended to scatter. Those leaving mats of *H. undulatum* in the dunes must have moved rapidly away; many must have lost touch with their fellows, but a proportion found their way into the millet. Those scattering in zone III wandered slowly unless entering a very bare zone (Ia or Ic). Many dispersed without reaching the concentration zones but, as much of III contained hatching sites within 30 m. of millet, many must have reached it, especially if they came within say 10 m., where visual attraction would direct their wandering to it.

Hoppers at 50 m. or more from the millet tended to collect in the vegetation with the maximum horizontal and vertical density (preferably with bare patches) and sometimes formed local concentrations if vegetation density differences were marked. In millet, older hoppers tended to concentrate less than young ones, since they wandered to a small extent into clean millet.

Two important factors accentuate concentration tendencies. Firstly, while most hoppers were in the later instars vegetation was beginning to dry up, especially in II and III, both beginning to approach the vegetation density of Ic or even Ia. Consequently, wandering is accelerated and concentration increased by the reduction in size of the well-covered zones. Secondly, sporadic weeding, particularly among the millet, causes a similar acceleration of concentration. Hence the concentration range may be extended sometimes beyond 50 metres.

The wandering rate in unweeded millet, while undoubtedly low, is difficult to estimate. Local concentrations within uniformly dense millet were not noticed. Hoppers probably spread gradually until more or less uniformly distributed, for the millet fields were never extensive. Thus the degree of concentration presumably depends on the size of the patch of the concentration zone in relation to the number of hoppers present.

Unweeded millet constitutes the commonest type of concentration zone on the Sudanese coast of the Red Sea (Maxwell-Darling, 1936). The apparent reason for this is that unweeded millet is the type of zone the vegetation of which differs most from that of all other zones in its height, and dense, but irregular, undergrowth. In the absence of millet, concentrations occurred where vegetation of a similar type was found (pl. 4, fig. 7, and pl. 5, fig. 8). Thus, while a concentration zone must have a certain minimum density and size, the "concentration value" of a given patch is not to be judged by the absolute conditions,

but more by the qualitative and quantitative relations between it and neighbouring zones.

That wandering by young hoppers seems insignificant means that only two or three weeks are available to any one hopper to contribute to Real Concentration, and the amount achieved by the first generation is appreciable and important, but its cost great, owing to the great decrease in numbers and the loss of innumerable individuals unsuccessful in reaching a concentration zone. Unless the adults of this generation add greatly to the concentration it is easy to understand that the production of a second winter generation and the consequent Virtual Concentration of that generation is an essential pre-requisite of an outbreak.

2. Adults.

Data on movements and concentration of adults are scantier than on hoppers. Early in the investigation attention was centred on hoppers. The disappearance of most of the first winter generation adults by the end of February was unexpected and plans for investigating their movements had to be abandoned. In the latter half of March and outset of April Hamashiameb was re-populated by *dissocians* adults, offspring of the second immigrant swarm. Most were derived from hoppers which had not been in band formation since their second instar. Most observations on various aspects of adult concentration described below were made on *dissocians* adults.

(i) Adult distribution.

Only a specimen or two of old, sexually mature adults was found; the majority must have died after egg laying. Thus the distribution of indigenous adults was initially the same as that of the older hoppers.

It was concluded from observations on hopper movement that by the time of the last moult a fair proportion of surviving hoppers would be concentrated in unweeded millet, so that many of the first winter generation adults were in what was for them also a concentration zone. Many other adults would, however, reach this stage away from cultivation, in local concentrations in zone III.

Counts of the recently moulted indigenous adults were made in January, but were inadequate to provide a picture of adult distribution which can be judged from what has been said of the distribution of older hoppers. Some figures may indicate the order of population density.

For lack of time and assistance adult counts could not be based on captures, and the method was to walk 110 metres across the wind, noting the number of locusts. Usually three 40-pace traverses, 13 paces apart, were made so that locusts in about 1330 square metres were counted. Where locusts rising were too numerous to count an estimate was made in tens or fifties. The figures cannot be converted even into roughly estimated actual population densities, but the adults were certainly much fewer than the hoppers which preceded them, as was noted by Maxwell-Darling (1936).

Counts on bare zones (Ia) even close to dune edges and millet gave only 1-5. Locusts were numerous on bare ground along the borders of cultivation, but always returned to the millet for the night and cannot be regarded as occupying zone Ia; after strong wind adults could be found on bare ground to the leeward of millet; obviously they had been carried by the wind and apparently returned. In zone III, the most extensive in the flood course apart from millet cultivation,

counts of young adults gave 30–200 according to vegetation density. As with older hoppers, adults were most numerous in millet. Counts in unweeded millet west-north-west of camp gave 450–600 and even more in the millet in Khor Toqwan. Unlike hoppers, adults were very numerous also in millet entirely without weeds. West-north-west of the camp where *H. undulatum* mats and patches of zone III adjoined clean millet counts gave 200–400. Very few

TABLE XVIII.

Counts of *dissocians* adults.

Sym- bol	Vegeta- tion zone	Particulars	No.
3.iv. A–H contiguous, in and around the extreme northern end of the cultivation in Khor Toqwan (as hopper counts on 23.ii., Table VI). H–K contiguous with the main unweeded Khor Toqwan millet field (as hopper counts 20.ii., Table VI). L and M in and beside the cultivation in the middle of Khor Toqwan. N–Q in and around the largely clean and still green millet near the western mouth of Khor Toqwan.			
A	IVc.	The strip of once very dense irregular vegetation, forming the extreme northern edge of the cultivation here (hopper count C, 23.ii.).	350
B	Ib.	Dunes west of count A.	17
C	II.	Dense grass, now trampled, south of count A.	25
D	Ic.	Principally <i>Suaeda</i> and <i>Panicum</i> bushes, east of count A.	20
E	Ic–IVb.	Thickly growing <i>Panicum</i> bushes adjacent to main millet field.	28
F	IVc. (poor).	Scanty millet with thick grass and dry <i>H. undulatum</i> .	33
G	Ic–II.	Scanty millet, small <i>Suaeda</i> bushes, patchy grass.	13
H	IVc. (poor).	Thin millet with small <i>Suaeda</i> bushes and very thick grass.	75
I	IVb.	Fairly thick clean millet.	210
J	III.	Small thickly growing <i>Suaeda</i> bushes only, west edge of millet field.	0
K	IVa.	Tall thickly growing <i>Suaeda</i> bushes and scanty grass.	25
L	Ic.	Chiefly <i>Panicum</i> bushes.	35
M	IVc.	Thick but drying unweeded millet.	300
N	IVb.	Very thick green clean millet.	1,850
O	IVb.	Fairly thick green clean millet.	970
P	IVc.	Thin green unweeded millet.	900
Q	IVa.	Thickly growing <i>Suaeda</i> and <i>Panicum</i> bushes in west opening of Khor.	25
6.iv. North-east of the camp and in the "Unnamed Khor."			
A	Ia.	Open plain between camp and La'at.	1
B	IVb–IVc. (poor).	Scanty millet near Omargarab range.	9
C	Ic.	<i>Panicum</i> bushes only, western slope of Omargarab range.	0
D	Ic–III.	Principally <i>Suaeda</i> and <i>Panicum</i> bushes near mouth of "Unnamed Khor."	17
E	Ic.	Principally <i>Suaeda</i> bushes, south and adjacent to millet in "Unnamed Khor."	2
F	Ic–IVa.	Thickly growing <i>Suaeda</i> and <i>Panicum</i> bushes, east of millet in same khor.	39
G	IVb.	Fairly green clean millet in same khor.	375
H	Ib.	Dunes of the Dividing Range.	0

TABLE XVIII (continued).

Sym- bol	Vegeta- tion zone	Particulars	No.
12.iv. Distributed all over Hamashiameb, as indicated.			
A	Ia.	Hard sand mounds with dead <i>H. undulatum</i> east of Omargarab.	1
B	IVb.	Dead millet near Omargarab range.	6
C	IVb.	Less dead millet near count B.	30
D	Ic-IVa.	Uncultivated northern extension of Khor Toqwan, principally <i>Suaeda</i> bushes with few weeds.	5
E	Ib.	Dunes north-west of count D with very large <i>Suaeda</i> bushes.	3
F	IVc.	Same strip of once-dense irregular vegetation as count A, 3.iv., now very trampled and open but still providing better vegetation and shelter than anywhere nearby.	80
G	III.	Grass very much flattened, as count C, 3.iv.	0
H	Ic-IVb.	Clean millet by count G, very open and windswept.	1
I	IVa.	Thickly growing <i>Suaeda</i> dying undergrowth (as count K, 3.iv.).	10
J	IVc.	Dead unweeded millet, less dense than count I (as count M, 3.iv.).	25
K	IVb.	Green but short windswept millet.	0
L	IVb.	Dying but still greenish clean millet, mouth of Khor Toqwan (as count N, 3.iv.).	15
M	IVb.	Millet towards Harabai Wells, much still green, in better condition than anywhere else in Hamashiameb.	50
N	IVa-IVc.	Dead millet away from dunes south-west of camp, with numerous <i>Suaeda</i> bushes.	1
O	IVb.	Millet among dunes near count N, much quite green.	25
P	Ia.	Dunes south-west of count O, quite numerous <i>Suaeda</i> bushes.	0
18.iv. A-C at Wara Dibbab. E-I at various places in Hamashiameb.			
A	III.	Among the <i>Suaeda</i> -bearing mounds where hopper counts were made on 27.i.	6
B	Ic-IVc.	Completely dead unweeded millet.	3
C	III-IVc.	Dying millet and small numerous <i>Suaeda</i> bushes.	2
D	IVa.	Near cultivation south-west of camp, undergrowth dead.	0
E	IVb.	Still green millet among dunes south-west of camp (count O, 12.iv.).	20
F	IVb.	Greenish millet west-north-west of camp, locusts only near south-west border.	7
G	IVb.	Clean millet in Khor mouth (count L, 12.iv.), locusts again concentrated at south-west end of patch.	12
H	IVc.	Millet in main Khor Toqwan field (counts M, 3.iv., and J, 12.iv.).	10
I	IVc.	Strip of northernmost cultivation, still fairly dense, but millet nearly dead (counts A, 3.iv., and F, 12.iv.).	15

locusts were in the millet among the dunes towards Harabai Wells, where weeds were very scarce and which was removed from places of previous years' cultivation. Later, locusts began to filter into this millet from the contiguous Khor Toqwan cultivation.

In zone III, where local concentrations had been, newly moulted adults appeared, but hardened adults, a week or more old, were very rare. In fact

by the beginning of February, when indigenous adults were at a maximum, locusts were seen frequently only in IV (a, b, or c).

Counts of *dissocians* adults, offspring of the second immigrant swarm, were made in the first half of April, and some are included in Table XVIII. It must be remembered that by this time all vegetation at Hamashiameb had begun to dry up, and during April desiccation was proceeding rapidly. The different connotation to be given to zone IVb in April and in January is shown in pl. 5, figs. 9 and 10. In April the only vegetation to retain some of its earlier luxuriance was patches of clean millet on coarse soft sand along the dune margins, towards Harabai Wells in the mouth of Khor Toqwan and among the dunes south-west of camp.

Counts of *dissocians* adults in April have only an indirect bearing on the distribution of the first winter generation indigenous adults, for hoppers which gave rise to them almost all hatched in, or very near, the millet fields. The only interest of these counts is the information provided on relative density of more or less contiguous patches, and they confirm in general observations on indigenous adult distribution. For adults and hoppers vegetation density was the most important element of a concentration zone, although vertical height of vegetation appeared much more important for adults than hoppers and density of ground vegetation correspondingly less important. Zone IVa (thick large *Suaeda* bushes, without millet) seemed nearly as good as millet as a concentration zone for adults; this emphasises that the species of plant is not as important as density and height.

Questions of adult distribution, movements and concentration fall into two classes; firstly, why adults stay concentrated in millet without close relation to density of undergrowth; and secondly, what happens to adults scattered from sites of local hopper concentration in III, and whether many of them reach the millet, adding to concentration begun there by the older hoppers.

(ii) *The food factor.*

Like that of hoppers the distribution of adults seems not to be associated with particular food-plants. An experiment on adult food preference was carried out in mid-January. Twenty recently, but not newly, moulted adults were put, with a jar of approximately equal-sized sprigs of *Pennisetum typhoides*, *Heliotropium pallens*, *H. undulatum*, *Aristolochia bracteata*, *Suaeda fruticosa*, *Euphorbia* sp., and *Cenchrus* sp., in a cage and the amount of each plant eaten daily for three days noted; the plants were renewed daily. Results are given in Table XIX, where the plants are arranged in order of apparent preference. Again the only plant left untouched was the salt-bush *S. fruticosa*. Millet was apparently not preferred to *H. undulatum* (often occurring outside the millet fields), and *Euphorbia* and *Cenchrus* were somewhat eaten despite the presence of more favoured plants.

Absence of strong food-preference in *S. gregaria* adults, both solitary and gregarious, has often been demonstrated. Husain (1934) said "over 300 different plants were supplied to the desert locust and of these it refused to feed on about one dozen." Karandikar (1933a) described careful experiments on the Pasni "rek" (Baluchistan), and out of 9 plants listed 5 were sometimes rejected even at the cost of life, but were eaten at other times. *H. undulatum* was distinctly preferred, but *Suaeda nudifolia*, *Salsola* sp., *Ipomoea biloba*, *Alhagi camelorum*, *Acanthophyllum squarrosum* and other plants were eaten in the presence of *H. undulatum*. No preference for *H. undulatum* was notice-

able in the field at Hamashameb and it would not assist much in keeping them in concentration zones. Karandikar included no common grain-plants in his experiments but Ramchandra Rao (1937) found *Andropogon* preferred to *H. undulatum*, but data are few. Maxwell-Darling (1934) found *Sorghum vulgare* much eaten in northern Kordofan (Sudan) but not more than *Tephrosia obcordata*, *Melhanian denhamii*, and *Chrozophora oblongifolia*. Maxwell-Darling called *Schistocerca* "a very catholic feeder" compared with other ACRIDIDAE tested.

TABLE XIX.

Results of experiment on food preference of adults. Further explanation with Table VIII.

Plant	1st day	2nd day	3rd day
<i>Heliotropium undulatum</i> . . .	1	1	1
<i>Heliotropium pallens</i> . . .	1	1	1
<i>Pennisetum typhoideum</i> . . .	2	1	1
<i>Euphorbia</i> sp.	2	2	3
<i>Aristolochia bracteata</i> . . .	3	4	3
<i>Cenchrus</i> sp.	5	3	2
<i>Suaeda fruticosa</i>	5	5	5

With first indigenous generation adults still numerous, vegetation had begun to dry up, especially on the hard ground of the plain. For a 2nd winter generation this process would have advanced further. Consequently, the quality of food (water content) differed in different zones, and there is good evidence (Ramchandra Rao, 1936b, 1937, and Husain, 1934) that preferences based on water content are definite although not absolute. The influence of differences in water content in vegetation in different zones is a contributing factor in differential wandering rates (see 18.iv., Table XVIII).

In a 10-day experiment on mortality rates on different foods, 14 individuals were put in each of 5 cages, 4 contained only one of *P. typhoideum*, *H. undulatum*, *H. pallens*, and *Cyperus* sp., the 5th contained no food. In the last one or two locusts died daily and only 2 were left on the 10th day in spite of cannibalism. In the other cages there were very few deaths and no apparent difference in the number of deaths on different food-plants.

Maxwell-Darling's experiments (1936) showed no difference in rate of sexual maturation of *Schistocerca* adults on different diets, but Ramchandra Rao (1936b, 1937) claims that sexual maturation is more rapid on *Andropogon* than on *H. undulatum* and much more than on other plants. Effect of food on rate of sexual maturation can only influence prospects of a 2nd winter generation and hence of Virtual Concentration, probably having no influence on concentration of the 1st winter generation.

As with the hoppers, it seems impossible to allocate to the food factor anything but a subsidiary rôle.

(iii) Observations on adult movements.

Observations on adult movement fall under three main heads: experiments on normal and differential wandering rates, observations on visual attraction to conspicuous objects, and on taking-off and flights.

a. Wandering Experiments.

These were made in April, the only available adults being phase *dissocians*. They were not in swarm formation and their behaviour resembled that of the indigenous adults they had replaced.

The method was similar to that of the 3-day wandering experiments on hoppers. The adults were placed in a zone before sunrise whilst still sluggish and a man set to watch each till sunset, leaving labels to mark its path. New locusts were used daily. Some temperature and wind readings were taken in situations similar to those occupied by the locusts. Only in zones Ia (pl. 2, fig. 2) and IVb (pl. 5, fig. 9, and pl. 6, fig. 11), representing extremes regarding height of vegetation, were experiments made. Unlike those with hoppers, experiments were possible in IVb because of the inactivity of the adults. The average screen maximum for the experiments in Ia was 33.2° C. (31-35), and for IVb 32.2° C. (28-35). The average daily distillate in the Radio Integrator was 49 c.c. (30-64) for Ib, and 51 c.c. (39-56) for IVb. Daily changes in humidity were roughly similar for the zones.

Some results are given in Tables XX and XXI. One adult was used throughout the day except on 4.iv. and 10.iv. (1st case), when replacements were necessary. As with hoppers, the greatest single traverse of the day took place within an hour of the start in 8 of 11 cases in Ia, suggesting the effect of initial stimulus of handling and that distances were somewhat exaggerated compared with normal. This was not apparently the case in IVb.

It is striking that even in Ia the average daily travel was only 7 metres (min. 2.6 m., max. 17.2 m.). The average in clean millet (excluding movements on the millet stands) was much less than in Ia (4.6 m.) and in 3 cases no horizontal travel was observed, the whole day being spent on one millet stand. The distance from daily starting to finishing point was much less than the distance travelled, movements being inconsistent in direction even in Ia. In other observations 12 adults were stimulated to move by handling or high soil temperature; 8 moved upwind as the hoppers had done, and 4 walked straight to a near-by bush. The directions taken by less excited locusts in the wandering experiments were nearly random.

Concerning factors in wandering, the case appears different from that of the older hoppers, since in Ia more time was spent on the ground than on vegetation. On this zone adults sometimes appeared to be sheltering from the wind, but usually their position seemed unrelated to the wind or to temperature. Rather more movement occurred on the ground than on vegetation; this is probably connected with considerations of wind and foothold, but it was obvious that this influence was much weaker for adults than hoppers. Two individuals spent the whole day on the ground (5.iv. and 25.iv.) although often not in the warmest or best sheltered position available.

In millet, however, most time was spent on the stands despite the warmth and windlessness of the ground; this does not agree with all-day observations on behaviour of large numbers of locusts in clean millet (see Aggregation). When, as in the latter, no regard was paid to individual behaviour the impression was that the majority of adults spent most of the day on the ground, but not so large a majority as of older hoppers. These generalised observations are probably subject to error, for locusts on the ground are more conspicuous than on plants, and one may wrongly imagine there are fewer on the plants than are actually there. Maxwell-Darling (1934) made similar observations on the individual adult *solitaria* of *Schistocerca* in Kordofan; the locusts he observed

kept all day to positions where the "sun temperature" was 38-42° C. He does not state on how many these findings are based, but if his number was larger than mine the apparent contradiction is perhaps less surprising. In 3 cases (second case on 8.iv., on 12.iv. and 24.iv.) most time was spent on the ground.

During these observations high midday temperatures were common and it was noticed that at midday, when and where sun temperature 1 cm. from the ground was over 40° C. and soil temperature over 50° C., locusts were never on the ground. Some observations were made on adults placed on the ground at midday with temperatures in excess of these. Most took to flight immediately, probably in response to handling, but 12 which remained raised one foot after another from the hot sand and moved off within a minute or two, eventually reaching and climbing bushes. Similar reactions with a soil temperature of 50° C. are recorded by Maxwell-Darling (1934). Such temperatures are rare in January and February when indigenous adults are present at Hamashiamab, so their potential accelerating rôle in wandering on bare zones is not large. For a 2nd winter generation high midday temperatures are frequent, but since this generation would be mostly concentrated in millet, high temperatures would play no important part in concentration.

The little information on micro-climates in relation to behaviour does not merit detailed consideration, especially as the wandering rate in both zones was so low that differences appear irrelevant to the question of concentration.

Differences in wandering rate seem connected with vegetation density because of the "braking" effect.

There is insufficient evidence for conclusions as to the existence of visual attraction to vegetation in walking or flying adults.

Eight cases only of flight were observed in all cases listed in Tables XX and XXI, and none exceeded 3 or 4 metres, but the instances are too few to draw conclusions. Near Tokar, where the only vegetation was large bushes of

TABLE XX.

Results of all-day wandering experiments on adults in Zone Ia.

Date	No. of locusts used	Duration (hours)	Actual distance (m.)	Straight from starting to finishing point		Proportion of 10 hours spent	
				Distance (m.)	Direction	on ground	on vegetation
3.iv.	1	8	17.2	0.9	SSW	6.9	3.1
5.iv.	1	8½	8.1	6.2	N	10.0	0.0
10.iv.	2	12	13.9	2.8	NNW	9.7	0.3
10.iv.	1	12	10.0	9.5	NNE	1.3	8.7
14.iv.	1	11	6.5	4.6	NNE	8.6	1.4
14.iv.	1	11	6.1	4.4	SE	5.5	4.5
14.iv.	1	10	4.0	3.2	ENE	2.0	8.0
14.iv.	1	10	3.8	2.4	SE	1.7	8.3
15.iv.	1	12	4.5	3.7	NNW	8.3	1.7
15.iv.	1	12	4.5	4.4	N	7.5	2.5
25.iv.	1	11	2.9	2.7	WNW	7.7	2.3
25.iv.	1	11	2.6	2.2	E	10.0	0.0
Means	—	—	7.0	3.9	—	6.4	3.6

TABLE XXI.

Results of all-day wandering experiments on adults in Zone IVb.

Date	No. of locusts used	Duration (hours)	Actual distance (m.)	Straight from starting to finishing point		Proportion of 10 hours spent	
				Distance (m.)	Direction	on ground	on vegetation
4.iv.	2	8	8.0	6.6	WSW	2.5	7.5
8.iv.	1	12½	0	—	—	0.4	9.6
8.iv.	1	12½	5.4	?	?	7.2	2.8
12.iv.	1	12½	0	—	—	4.8	5.2
12.iv.	1	12½	23.4	8.4	WSW	6.0	4.0
16.iv.	1	11½	0	—	—	0.0	10.0
16.iv.	1	11½	1.0	1.0	ENE	2.2	7.8
24.iv.	1	11½	1.5	1.3	SSE	5.8	4.2
24.iv.	1	11½	2.0	1.4	NNW	3.3	6.7
Means	—	—	4.6	2.4	—	3.6	6.4

Leptadenia spartium, 2 or 3 metres high on mounds at long intervals, unhandled *dissocians* were observed to make "spontaneous" flights up to 10–12 metres about midday when soil surface temperature exceeded 50° C., but in the better-covered zones at Hamashameb such flights were very short and the average daily number of flights per locust was much less than one.

Apparently, therefore, if the above observations on the low wandering rate of undisturbed adults bear much relation to reality, a quite negligible contribution to concentration is made by the adults.

The relation of these observations to actuality is not close, since disturbance from man and animal was obviated in the experiments although normally very common in and outside cultivation. Disturbance makes a hopper hop rapidly, but only so far as the first vegetation; the effect on an adult is quite different, for, unless newly moulted, it flies for several metres. Consequently the daily range of movement of an adult may be greater than that of a hopper. It is impossible even roughly to estimate the daily range of adults with normal disturbance, but the increase in daily range re-opened the question of possible contribution of adults to concentration.

The effects of disturbance are thought not to enhance the rôle of differential wandering rates in concentration. The length of disturbed flights in millet was not much less than in barer non-concentration zones. Moreover, disturbance by man was more frequent inside the millet, and probably assisted materially in dispersing adults from millet with weeds into clean millet.

If disturbances alone caused adult movement the whole adult population would become dispersed from the hoppers' concentration zones and drift south-west, as each short flight tended to carry the locusts a little with the wind. With a visual attraction to vegetation and the range of movement given to adults by disturbances a good contribution is made to concentration.

b. Observations on visual attraction.

The testing of adults for visual attraction by the careful methods used for hoppers was abortive because of low activity of adults; other sources of

evidence are therefore given. Evidence was difficult to obtain on visual attraction of objects for walking adults, as so little walking was done, but in observations near Tokar at midday, 12 cases of walking for a number of metres were observed. Locusts were placed on bare sand by a crouching observer 10 metres from a very large mound bearing *Leptadenia* bushes, similar mounds being present on all sides, 50–100 m. distant. Six walked north-north-east into the wind and continued out of sight. The remaining 6 reached the mound and climbed on the bush; one of them started 10 m. east of the mound and walked straight to it across the wind; three others started to the south of the mound, where there was almost no wind, walked straight to the mound; another also started to the south, walked first north-west but when within 6 m. turned and went straight to the bush across the wind; the remaining one started to the south, walked 2 m. east and turned back across the wind to the mound. These few cases suggest that adults are susceptible to attraction by a bush.

All other observations refer to flying individuals. In the above observations, 3 of 21 locusts which immediately took off when placed on the ground flew straight to the bush and alighted. The same day 2 resident, unhandled locusts were seen to make flights from the ground to an acacia tree across the wind. Other cases of spontaneous or semi-spontaneous flights to bushes were observed, but the directing influence of the wind could not be excluded, since the bushes lay upwind of the locusts. The wandering experiments on Ia were at a point 100 m. east of camp, which consisted of a group of white tents and darker grass huts, the tallest some 3 metres high. At 06.00 hours on 14.iv., 6 adults, intended for wandering experiments, took off a few minutes after release; 4 flew out of sight south or east, but 2 of them flew first north-west, roughly into the wind, circled back and settled on a hut.

More convincing evidence was obtained when attempts were made to drive locusts from their concentration zones; these were made with *dissocians* adults on 4 days in March. An adult in the millet was selected, disturbed and caused to fly, where it alighted was noted, and it was disturbed again until it reached the edge of the millet and alighted on the barer ground outside. Often it took off again without further disturbance and returned to the millet; if not the observer approached keeping between the locust and the millet. Despite this the locusts flew back to the millet regardless of the direction of wind or sun. This happened in all but 4 of about 50 observations; the locusts seemed drawn to the millet field as if attached by elastic. The same results were obtained in IVa, dense *Suaeda* bushes. Observations on diurnal movement (see Aggregation) suggest that attraction to millet affects less excited adults (either walking or in flight). Many adults spent most of the day on bare ground adjacent to but outside the millet fields, but returned in the evening.

Such attraction in relation to sedentary populations of non-gregarious adults is unmentioned in the literature, but cases of possible visual attraction of swarms to conspicuous objects are mentioned. Predtechensky (1935), describing the settling of a *S. gregaria* swarm in the evening, said that most settled on trees, telegraph poles and among dense vegetation on the ground, describing this as an apparent attraction. He also described diurnal flights of swarm adults from trees to the ground and back. As with similar flights from and to millet mentioned above, the descent to the ground may be explained by rising activity, but return flights to vegetation strongly suggest visual attraction. Andrews (1915) said *S. gregaria* swarms in India settled on a roof painted red but not on an adjacent unpainted galvanised-iron roof. Sviridenko (1924) suggested the return of individuals of *Dociostaurus maroccanus* Thnbg. to an

oasis from which short flights were made was due to the attraction of green vegetation, but visual attraction may also be suspected. Cotterell (1930) wrote that when the country (Gold Coast) was drying up *L. migratoria migratorioides* swarms tended to settle by swamps and rivers where vegetation was still dense. This he associated with the food available there, but unless the locusts can sense vegetation by smell or other means, visual attraction again seems more probable. Lépiney (1928) recorded the attraction of members of settling swarms of *S. gregaria* to conspicuous objects such as trees, emphasising, what is not so clear in some cases quoted above, that the attraction is apparent well before any effect which the trees may have had on the air over them could have been felt by the locusts.

On the whole, there is good evidence that visual attraction to conspicuous objects is widespread in locusts. Its importance in concentration at Hamashiameb was evidently great. It provided an explanation of the fact that locusts remained concentrated in millet in the adult stage, and probably assisted them to reach the millet from other zones, in the course of their sporadic disturbed flights.

c. Observations on spontaneous taking-off.

The above observations seem inadequate to explain all apparent movements of adults at Hamashiameb. As mentioned under Locust Population, a diminution of locusts not easily ascribable to normal causes occurred twice; in the first case indigenous adults at the beginning of March were found to be less than one-fiftieth of those at the beginning of February. By the end of March indigenous adults were taken only rarely. During February the second invasion of immigrants passed through Hamashiameb. While in cultivation this swarm intermingled with indigenous adults; the locusts were very restless, making short loose flights, and some trickling away daily towards the north in small low-flying scattered swarms. Indigenous adults were not counted in February, but possibly some were "picked up" and flew away with the swarm. If so, this observation is of no great interest in the matter of movements of an indigenous population, but it is possible that indigenous adults took off and flew away of their own accord. In the second case, *dissocians* adults, offspring of the second immigrant swarm, in 3 days dropped to one-tenth of their initial number (3-6.iv.). The locusts were living solitarily and no swarms were present at the time, but emigration seems the only explanation, which receives support from the numbers attracted to light at camp (800 m. from nearest cultivation, and 1500 m. from the main Khor Toqwan cultivation where most adults were); during this time these were much greater in the evening than usual, suggesting that the locusts were on the move. If migration was taking place by day also it is surprising that it was unnoticed.

If emigration be the explanation, sustained flights must have been more frequent than other observations had suggested and the possible rôle of such flights in concentration had to be considered.

Disturbed flights of more than 10 m. were not observed, although a cultivator who spent much more time in the cultivation than we, reported in the first few days of March seeing 20 of the numerous *dissocians* adults disturbed by him, rise high and fly out of sight. Most of these flights took place about sunset. Ramchandra Rao (1936a *et seq.*) and Zolotarevsky and Murat (1938) have observed forced taking-off to be followed by long flight, and sometimes a headlong passive descent after the locust had risen high; this last was never observed at Hamashiameb.

Maxwell-Darling (1936) said that disturbed flights are usually short. With such inadequate evidence of disturbance causing sustained flight, attention was concentrated on the possibility of spontaneous taking-off. The evidence of Ramchandra Rao and his co-workers (1936a and b, 1937) on the migration of solitaries in Baluchistan encouraged the idea of spontaneous taking-off and sustained flight on the Sudanese coast.

In the 21 wandering experiments described above only 8 cases of true spontaneous flight, all very short, were observed. On 25.iv. a released locust pottered about for half an hour, took off, rose high and flew out of sight soon after sunrise. Mass behaviour of adults in millet suggests that "spontaneous" taking-off of a minority of individuals occurred morning and evening, although the take-off was seldom observed. Flights were short and irrelevant to the question of spontaneous sustained flight. If such short flights occur in non-concentration zones, they may assist concentration by increasing the range of movement of adults, much as disturbance did.

A chance observation after sunset on 25.iv. is of great interest. Caged locusts at camp had been fed at sunset and a cage door was left open. The observer sat a few metres away and no lights were visible except that of the western sky. The air temperature was 29° C. and humidity about 75%; a gentle north wind was blowing. Between 30 and 50 minutes after sunset 10 *dissocians* adults emerged one by one from the cage, climbed slowly and paused on top of the cage; after a few moments they turned so as to face west. After a further short pause, 5 took off and flew out of sight (visibility not more than 80 m.) towards the west. Two more flew first to the ground, turned west and took-off. Two others flew 20-30 m. west, turned and flew north-east back to the hut and settled. The remaining one took-off westwards, flew 10 m., turned and flew south downwind. This suggests that spontaneous taking-off and fairly sustained flight may be stimulated by directed light of low intensity.

Tests at other times of day were negative. Cages were set up, their lids removed with care, allowing the locusts to crawl out, twice before sunrise and once at midday. In one of the sunrise experiments no take-off occurred; in the other locusts were accidentally disturbed and several take-offs caused, but no sustained flight was made and most flights were directed to a large bush upwind to the north. No take-off occurred in the midday experiments.

One evening an hour and a half after sunset a car was driven without lights to within 5 m. of a millet field in which were numerous locusts. The lights (about 200 metre-candles at 5 metres) were turned on. Locusts visible on millet stands tended to take up positions exposed to the light and broadside to it; in the next half-hour 20 flew off into the lights. It is worth recalling the fact that locusts and other Acridids will often fly to light at night.

At Hamashiameb there were always locusts near camp, and the completely undisturbed, spontaneous taking-off (preceded by orientation to light if the resting area were large enough) of all phases was common. Inside the hut undisturbed locusts took-off to the lamp at night, but also repeatedly in the direction of the open door (facing south) during the day. Clearly, taking-off was unconnected with the lower temperatures, higher humidities, or particular quality or lower intensity of light associated with dusk or night in the open. Before sunrise light conditions are similar to after sunset, and taking-off was not observed or expected as locusts were always rather sluggish.

The interest in these observations lies more in the fact that directed light of low intensity induced taking-off, than that flights were directed to the light.

It is a question whether the general light intensity or the direction of the incident light was the essential stimulus.

Experiments on this and other points were carried out in a room in Tokar, about $5 \times 4 \times 5$ m., with windows on 3 sides kept closed and fitted with shutters, which, when closed, shut off most light from the room. The walls were light blue with a black band 50 cm. high round the bottom; in the middle of the fourth wall, was a black door. The room was bare and contained only the observer, who lay in a corner and only moved to make notes. Twenty locusts were introduced in the morning and notes taken of the number walking and taking-off, and of the direction of movements. The shutters were opened and closed for 20-minute periods; with all closed, light intensity was below the lower limit of sensitivity of the exposure meter (20 metre-candles), but with shutters open and the instrument directed to a window from the middle of the room a reading of about 500-metre candles was obtained. All experiments were made between 9.00 and 14.00 hours. Temperature varied between 29° and 31° C. and relative humidity between 50% and 60%. In experiments on 4 days there were 11 20-minute periods with 1 shutter open, 11 with 3 open, and 23 interpolated with all closed, of which 4, 4, and 8 were on a day when millet was set up in clumps in the room. Table XXII shows how variable was the activity of the locusts. The high level on 16.iv. seemed to occur because observations were started too soon, and a longer period of adjustment was allowed on subsequent days. In the experiment with millet, activity was always at a low level, and its increase by open shutters was manifested principally in locusts climbing stems (not indicated in Table XXII). The behaviour can only be compared in successive 20-minute periods, and a single set of figures showing relative activity under each condition of illumination could not be extracted.

The opening of the shutters greatly increased activity, including taking-off, but this was not confined to the moment of opening, and the response does not appear to be connected simply with it. In both conditions where light was admitted, flights were mainly towards the source of light. Even with all shutters closed flights were towards parts illuminated by chinks in the shutter louvres. On the floor, orientation after opening the shutters was usually towards the source of light, as was walking, but subsequently many locusts walked to dark corners or the black door. On the millet they took up positions illuminated by, and perpendicular to, the light rays.

The experiments were inadequate and failed to give an answer to the main question. It was expected that more taking-off would occur with one than with all shutters open; this was not so, but unfortunately there were always marked differences in the illumination of different parts of the room.

The observations, however, emphasised the complexity and delicacy of reactions to light; walking and flying to the light, and walking to dark corners could be seen simultaneously in different individuals under identical conditions, and immediately following one another in the same individual. It emerged from the experiments that although walking to and from lighted places was observed, flying was usually towards the light and never consistently away from it to darker places.

Considering all observations described in this section, it is concluded that spontaneous taking-off occurs most readily when general light intensity is low and the intensity of light incident from various directions markedly different.

In the indoor experiments, where light intensity was never high, an increase in intensity resulted in more frequent taking-off, but adults emerging

TABLE XXII.

Results of experiments on the effect of sudden changes of illumination on taking-off by adults. Each figure is the total for 30 minutes. Arranged in chronological order. 16.iv., 20.iv. and 21.iv. in completely bare room; 19.iv. with millet clumps set up in the room.

Date	Conditions of shutters, and number of locusts moving								
	All shut			One open			All open		
	Walk- ing	Fly- ing	Total	Walk- ing	Fly- ing	Total	Walk- ing	Fly- ing	Total
16.iv.	152	61	213	—	—	—	—	—	—
	—	—	—	—	—	—	117	75	192
	51	13	64	—	—	—	—	—	—
	—	—	—	111	43	154	—	—	—
	48	33	81	—	—	—	—	—	—
	—	—	—	83	35	118	—	—	—
	14	13	27	—	—	—	—	—	—
	—	—	—	—	—	—	34	20	54
	39	16	55	—	—	—	—	—	—
20.iv.	—	—	—	—	—	—	68	20	88
	18	4	22	—	—	—	—	—	—
	—	—	—	52	21	73	—	—	—
	26	1	27	—	—	—	—	—	—
	—	—	—	—	—	—	65	6	71
	22	0	22	—	—	—	—	—	—
	—	—	—	18	1	19	—	—	—
	15	0	15	—	—	—	—	—	—
	—	—	—	—	—	—	18	2	20
21.iv.	9	0	9	—	—	—	—	—	—
	—	—	—	18	0	18	—	—	—
	98	10	108	—	—	—	—	—	—
	—	—	—	—	—	—	109	10	119
	31	3	34	—	—	—	—	—	—
	—	—	—	68	10	78	—	—	—
	10	0	10	—	—	—	—	—	—
	—	—	—	—	—	—	35	7	42
	22	0	22	—	—	—	—	—	—
19.iv.	—	—	—	56	3	59	—	—	—
	—	2	—	—	—	—	—	—	—
	—	—	—	—	—	—	—	13	—
	—	2	—	—	—	—	—	—	—
	—	—	—	—	3	—	—	—	—
	—	0	—	—	—	—	—	—	—
	—	—	—	—	—	—	—	1	—
	—	0	—	—	—	—	—	—	—
	—	—	—	—	1	—	—	—	—
	—	0	—	—	2	—	—	—	—
	—	—	—	—	—	—	—	—	—
	—	0	—	—	—	—	—	0	—
	—	0	—	—	1	—	—	—	—

from the dark pit, used in visual attraction hopper experiments, into bright sunshine did not take-off, and spontaneous taking-off in the field was rare in daytime. If taking-off is a simple photokinetic response (direction towards source of light being incidental) it seems associated with a particularly low level of light intensity, for it does not take place above or below that intensity.

If intensity alone is responsible for taking-off, if, that is, it is a simple photokinetic response, then it appears to be the sole activity of locusts particularly associated with such a light intensity. Locusts are not normally crepuscular, although Everly (1929) found jumping in *Melanoplus differentialis* at a maximum at dusk, and, as his cages were kept in front of a window, the light was as much directed at midday as at dusk. Locomotion by walking, feeding, copulation, etc., are most frequent in the field during daytime, when light intensity is high and it is surprising that one form of activity should be associated with low intensity; this may be so, but observations suggest that the additional factor of directedness of the incident light is in itself a stimulus to taking-off.

Accidents of cloud formation in the evening, especially a cloud bank over the entire sky except the western horizon, sometimes resulted in sudden and great increase of illumination in the west as the sun appeared for a few moments before sinking and markedly accentuated the unevenness of illumination after sunset. It is suggested that such accidental events may in part account for the widespread taking-off presumed to be the cause of the rapid diminution of locusts at Hamashameb. The suddenness of the disappearance of the *dissocians* adults is itself an argument against simple photokinesis as the basis of taking-off.

The only case where I know this theory to be explicitly stated is Strelnikov's (1936b) account of factors determining taking-off by *Loxostege sticticalis*. In this moth, day flights are short and low but "... die stärkste Reaktion bekunden die Falter im Fliegen gegen das Licht. . . . In einer gleichmässig beleuchteten Umgebung ist eine solche Flugreaktion nicht zu merken." Taking-off followed by sustained flight by the moth was observed mainly from 40 to 50 minutes after sunset until the appearance of the first stars. While mentioning unequal distribution of illumination as a cause of taking-off, he does not distinguish between such response and photokinesis, and the suspected stimulating effects of directed light remain unproven. *Loxostege*, like *Schistocerca*, is not particularly crepuscular except in taking-off.

Ramchandra Rao (1936a and b, 1937a) has given most attention to taking-off followed by sustained flight in solitaries. He and his co-workers have accumulated evidence pointing clearly to migration flights among indigenous *Schistocerca*, and the disappearance of locusts from Hamashameb suggests that this may not be confined to Baluchistan. Zolotarevsky and Murat (1938) record the sudden disappearance of *Schistocerca*, of which emigration seems the only explanation. As to conditions of taking-off, it appears that flights were observed in disturbed and undisturbed locusts, but it is interesting that dusk is the time mentioned by Ramchandra Rao as associated with taking-off. Flights were obviously not passive, "each individual being noted to steer its course in a particular way," but it is not clear whether there was uniformity in direction faced by the locusts or any relation to the illuminated western sky.

He mentions some observations of apparently spontaneous taking-off and high flying at midday; this was not observed at Hamashameb but is highly feasible with high soil temperatures and no conspicuous vegetation.

Maxwell-Darling (1936) also described spontaneous taking-off and "flying

about" at dusk of *L. migratoria migratorioides congregans* in small, non-migratory swarms at Khor Arbaat on the Sudanese coast in winter 1931-32.

Rockwood (1925) and Golding (1934a) record night flying of ACRIDIDAE (other than locusts) and attraction to light during such flights. Both mention high evening temperature as associated with flights. Spontaneous taking-off at dusk and on into the night appears to be widespread among Acridids, not otherwise crepuscular or nocturnal insects. In semi-gregarious *Calliptamus turanicus* Tarb., flights occur in the day (Zimin, 1934), as in true gregarious locusts, within certain temperature and wind velocity limits. Wind gusts are mentioned as stimulating taking-off.

Taking-off by members of swarms cannot give information regarding solitaries, since the responses of a locust to its neighbours plays the largest part (Uvarov, 1921, 1928; Lépiney, 1928, 1930c; Johnston and Maxwell-Darling, 1931; Fraenkel, 1932). Temperature is the next most frequently cited factor, flights taking place mainly in the daytime. Olsuf'ev (1930) found that taking-off for the first flight by young swarms of *L. migratoria* occurred more at sunset than at other times, and as days became warmer, taking-off occurred later, at dusk, sunrise and after. With high temperatures, night flying by swarms is common (Uvarov, 1928).

There appear good grounds for supposing that taking-off and sustained flight is especially associated with light conditions at dusk, whether this is simple photokinesis or not.

d. Observations on direction of flight.

If individual spontaneous taking-off be followed by sustained flight, the direction taken would be of great interest.

The only direct observations made, were on the locusts which escaped after sunset on 25.iv. These orientated towards the illuminated western sky. The direction of flight varied between almost due west and south-west; there was a slight wind from the north.

Before this, observations had been made on the direction taken by individuals forced to take-off by handling, since spontaneous taking-off was so rare. Evidence on the directions taken, had the take-off been spontaneous, were hoped for from these observations.

All locusts used were *dissocians* and the methods were not all uniform. The releaser was usually largely concealed, and men crouching at a distance helped in determining flight direction and body orientation.

The results are summarised in Table XXIII. The inconclusiveness of many results make them not worth quoting. Wind strength averaged about 7 m./sec. in all observations. Of the 7 sets of observations made, one was about sunrise, one in mid-morning, one at midday, two in the afternoon, and two about sunset. The total in each category varied between 117 and 135, as all aspects of flight direction were not always noticed. The data all apply to directions assumed after the initial take-off was over and a more or less steady state, and height of over 10-15 m., attained. Directions are approximate, being sometimes subject to an error of as much as 20°, and are those towards which the wind blew (due downwind = 0°, due upwind = 180°), towards the sun (straight to the sun = 0°, away = 180°), and towards which the flight or body was orientated.

The great majority of flight directions (category 1) were southwards, especially south-west. The wind being predominantly south or south-west,

TABLE XXIII.

Relation of flight directions and body orientation to external features, in forced flights.

Category	Distances (m.)	Quadrants of compass				
		NE	SE	SW	NW	
1. Flight directions	100 and over	3	25	67	14	
	30-90	0	14.5	8.5	3	
	Totals	3	39.5	75.5	17	135
2. Body directions	100 and over	19	28.5	30	13.5	
	30-90	13	10	2.5	3.5	
	Totals	32	38.5	32.5	17.0	120
		Deviations from wind and sun direction				
		0-10°	11-44°	45-134°	135-170°	171-180°
3. Flight directions and wind	100 and over	26	48.5	18.0	1.5	0
	30-90	0	7.5	17.5	0	4
	Totals	82		35.5	5.5	123
4. Body directions and wind	100 and over	6	26.5	44	6.5	4
	30-90	2	0	14	8	6
	Totals	34.5		58	24.5	117
5. Body directions and sun	100 and over	29	6.5	39	25.5	7
	30-90	0	0	10	10	1
	Totals	35.5		49	43.5	128

this is directly due to the situation shown by category 3, where the majority "flew" downwind. Flight was often downwind, even with the angle of body to wind direction being 90° or more. The strength of forward flight was thus usually inadequate to make much difference to effective flight direction in relation to the ground, and the locusts were largely carried by the wind. It is possible that in their highly stimulated state, forward flight was not so strong as normal, so that the orientation of the body, apart from effective flight direction in relation to the ground, deserves attention.

Orientation of the body upwind was usually the condition when close to the ground, immediately after taking-off or before alighting. This interesting observation is also reported in *Schistocerca* (Zolotarevsky and Murat, 1938) and *L. migratoria migratorioides* (Lean, 1936), and is difficult to explain except in terms of visual reaction to the movement of images of the ground pattern across the retinulae, as Fraenkel (1932: 203) and others suggest in relation to upwind flight of a number of insects. Unlike hoppers, with proprioceptors in the legs to respond to wind pressure on the body, flying locusts are presumably unable to relate direction of movement to the ground except visually.

The more interesting point is that in full flight 35 of 123 locusts faced neither

up- nor downwind but across wind, 45-134° from the wind direction. If these be fitted into Fraenkel's scheme, they cannot be regarded as related to direction of movement of ground pattern images as a whole, except in the unlikely contingency that each individual selected a particular direction of passages of images across its eyes and so orientated itself to maintain that direction. Fixation on a definite object, as the sun (Lépiney, 1928, sometimes observed this in *Schistocerca* swarms) or a feature of the landscape, was more to be expected. However, category 5, Table XXIII, shows no evidence of fixation on the sun, nor 2, any of fixation on a particular feature of the landscape.

The only conclusion from the observations, therefore, is that irrespective of body orientation, individuals tend to be carried downwind. Many also faced downwind. This may be due to the locust not having begun to fly strongly, or to have assumed a definite orientation, until out of sight. The strength of the wind and its usual direction on the Sudanese coast in the breeding season are such that locusts taking-off and flying some distance will be carried roughly south-west. This point is discussed later. Otherwise the observations add little to the still obscure question of the orientation of flights (Lépiney, 1928, 1930d, 1933; Zimin, 1934).

(iv) *Conclusions on adult concentration.*

Data on movements and concentration of the 1st winter generation adults, even supplemented by observations on *dissocians* adults, are insufficient to draw conclusions; the following are therefore provisional.

Behaviour of adults may be divided into two, and probably three, categories: normal undisturbed behaviour; disturbed behaviour; and abnormal undisturbed behaviour.

1. Undisturbed adults are usually inactive with small range of movement, much less than older hoppers. Differential wandering rates in different zones, therefore, cannot make appreciable contribution to the concentration process. There may be short spontaneous flights of several metres, but these appear rare.

2. Adults are subject to not infrequent disturbances under which influence their range of movement may be much more than that of hoppers. There is no marked difference in range of movement of disturbed adults in- or outside concentration zones, and allowing for disturbances, concentration due to differential wandering rates cannot be important, but adults are as susceptible to the visual attraction of conspicuous vegetation, constituting concentration zones, as are hoppers. With the range of movement given by disturbance, visual attraction probably assists adults to continue the concentration into millet begun by hoppers, and, in the millet, to prevent scattering out of it.

3. "Abnormal undisturbed behaviour" is taking-off followed by more sustained flight than is usual. Evidence of sustained flight as a result of disturbance is poor, but there are indications that in special circumstances (light and temperature at dusk may be the most important) spontaneous flights of at least 80 m. may occur. While the body orientation in any flight may be across wind, the effective direction is probably in the same quadrant of the compass as that towards which the wind is blowing.

With these points in mind, one may consider the actual concentration process of 1st winter generation adults (see Table VII, p. 412).

On completing their final moult many adults were in zone IVa or IVc. They then spread ("de-concentrated") to a greater extent than the hoppers

into any near-by millet with no weeds, and under the combined influence of disturbances and wind gradually drift to the south-west end of their concentration patch. Lean (1936) described a similar tendency of adult *Locusta* to concentrate on the downwind margin of vegetation patches. Locusts are, however, prevented by visual attraction from leaving the concentration zone altogether.

Other adults completing their final moult in local concentrations in zone III tend to scatter, and some may reach a concentration zone (limiting distance also unknown) especially if this lie downwind.

Differential wandering rates seem negligible in adult concentration. Flights following spontaneous taking-off, if not more than 100 m., might assist concentration in an area like Hamashiameb, but only if a zone lay downwind from the taking-off point. This may have often happened at Hamashiameb, but, speaking generally, would be exceptional. The possible consequences of spontaneous flights being sustained for greater distances have no bearing on local concentration and are discussed later.

Visual attraction thus appears virtually the sole important and positive agent of local adult concentration.

To sum up, adults of the 1st winter generation are able to maintain concentration achieved by older hoppers, and perhaps add to it. Some "de-concentration" into clean millet took place, and the population slowly declined, so that even had no emigration occurred the conclusion suggested by hopper movements that a 2nd winter generation is an essential pre-requisite of an outbreak, seems inescapable.

3. Notes on the prospects of concentration among an assumed second winter generation.

(i) Local concentration and outbreaking.

Since a 2nd winter generation is agreed as necessary to produce an outbreak, an estimate of the prospects of concentration in this generation may be attempted, although it did not materialise at Hamashiameb in 1937. Had indigenous adults not disappeared in February, a 2nd generation would have been expected in March–April 1937.

It may be recalled that at end February 1st generation adults were numerous only in zone IV, particularly b and c. They were not confined to the millet, and spent much time on adjacent barer ground. As desiccation of the vegetation proceeded in March and April, millet on harder ground away from the dunes and in the northern half of the cultivated part of Khor Toqwan could no longer be classified as zone IVb or c, and locusts were not common in it (Table XVIII). Millet on soft sand at the margins of the dunes remained green, with numerous *dissocians* adults.

The following is conjectural. Presumably, 1st generation adults lay eggs partly in, and partly close to, but outside, the millet. Millet in the dunes is never in large continuous fields, but in small patches interspersed with bare soft sand, so that by the action of the wind (Maxwell-Darling, 1936) the moist sand of the deeper layers suitable for oviposition is readily accessible in many places. Where mats of *H. undulatum* are present in, or near, the millet, doubtless many eggs would be laid close to them, for it grows on low ridges and mounds at the base of which moist sand is exposed by the wind.

Young, 2nd winter generation, hoppers hatching in such places would remain near millet and collect on available *H. undulatum* mats. In the absence of this,

hoppers would remain in the clean millet owing to its visually attractive influence. In the later instars, those on *H. undulatum* mats outside the millet would tend to scatter and, with some losses, concentrate in the near-by millet. Those in millet would remain, as would ensuing adults.

While the millet is green and produces new heads, cattle are not admitted, but their admission to cultivation elsewhere rapidly produces the condition shown in pl. 5, fig. 10, and even further until vegetation density approaches zone Ic or even Ia. This, added to the normal desiccation of the soil and vegetation in all zones, leaves the millet patches sharply demarcated and must increase concentration of hoppers and adults. Weeding the millet, which is still required, and sporadically executed in March, also assists in concentrating hoppers (not adults) as Maxwell-Darling (1936) suggested. Adult concentration in the millet may be increased by locusts being carried by the wind a short distance each time they fly in response to disturbance.

If the above be correct, the rôle of the 2nd generation in an outbreak is clearly seen.

"Real Concentration" due to active centripetal migrations over short distances, a wasteful process at best, takes place in the 2nd generation, in that movement from *H. undulatum* mats into millet and movements in relation to shrinkage of concentration zones seem very probable. Real Concentration in the 2nd generation must be much less than in the 1st, since the former start life in, or close to, concentration zones. Far greater contribution to concentration is made by the multiplication of individuals by the production of a new generation. The trapping power of concentration zones makes normal mortality the only factor tending to reduce the increased population density thus produced. In an outbreak year, mortality in the 2nd generation is necessarily inadequate to neutralise the effect of "Virtual Concentration" as I termed the events just described. In an outbreak, the rôle of the 2nd generation is thus not only in the multiplication of numbers; its members, forced to remain in the zones where they hatch, make an important positive contribution to concentration.

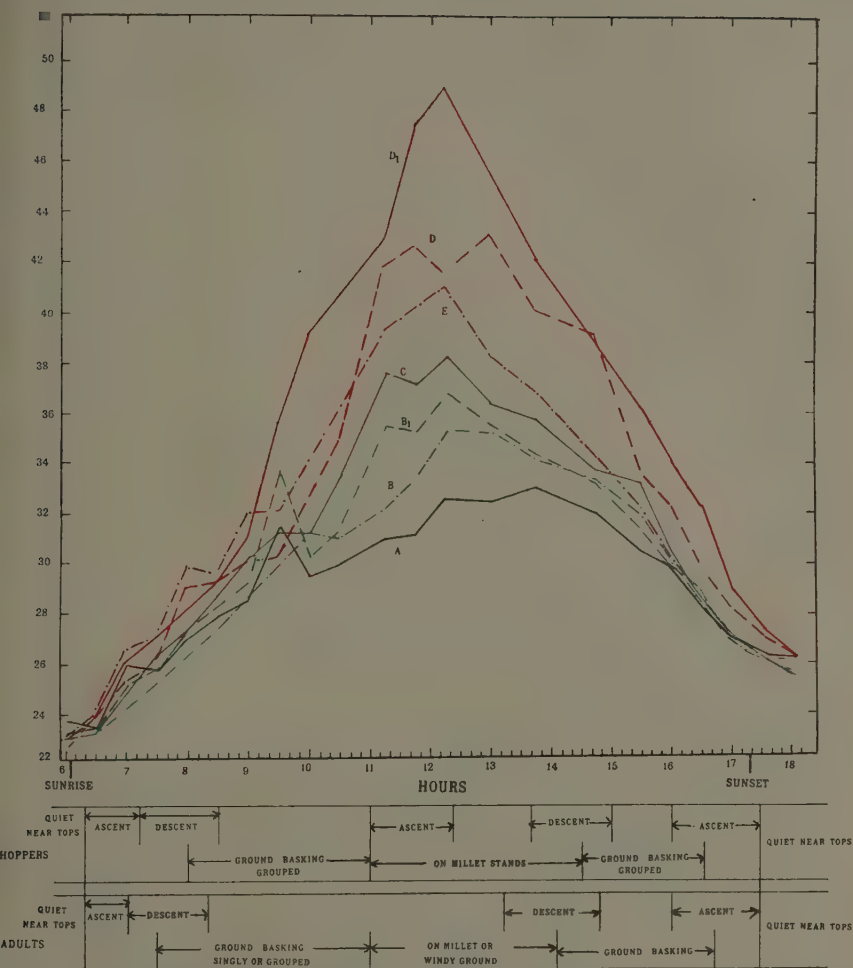
The production of an outbreak may thus be attributed to two events following one another: Real Concentration achieved by the 1st generation, and Virtual Concentration achieved by the 2nd.

(ii) Possibilities of larger-scale movements and concentration.

The remarks in this section are conjectural. Ramchandra Rao (1937a, *et ante*) believes non-gregarious populations in Baluchistan make individual migrations from one breeding area to another, leaving dried-out areas for those which have received rain. The "permanent reserves" of *S. gregaria* in Baluchistan are in many respects similar to those of the Sudanese coast. Evidence of solitary migration by *Schistocerca* in Mauritania has been advanced by Zolotarevsky and Murat (1938).

Some evidence of emigration of non-gregarious populations on the Sudanese coast has been obtained. Spontaneous sustained flights, even if not long sustained, will not usually contribute to local concentration, but if sustained for long distances and several days, then while having no bearing on local concentration, they would be of great interest in population distribution and possible large-scale concentration.

It was indicated that, with normal strength wind, flying locusts are carried with it, but this is open to correction. Ramchandra Rao (*loc. cit.*) reports it in individual flights observed by him and his co-workers, but points out that wind



Readings of unshaded plain thermometers ("sun temperature") at selected positions in unweeded millet during an unusually hot day in February (the 16th), and outline of behaviour of the majority of indigenous older hoppers and adults in the vicinity.

A: 1.5 m. off ground among millet heads (as pl. 6, fig. 11); wind speed at 14.00, 4.3 m./sec.

B: 90 cm. off ground among dense millet (pl. 7, fig. 13); wind speed at 14.00, 2.2 m./sec.

B₁: 60 cm. off ground lee side of clearing among millet (pl. 8, fig. 16); wind speed at 14.00, 2 m./sec.

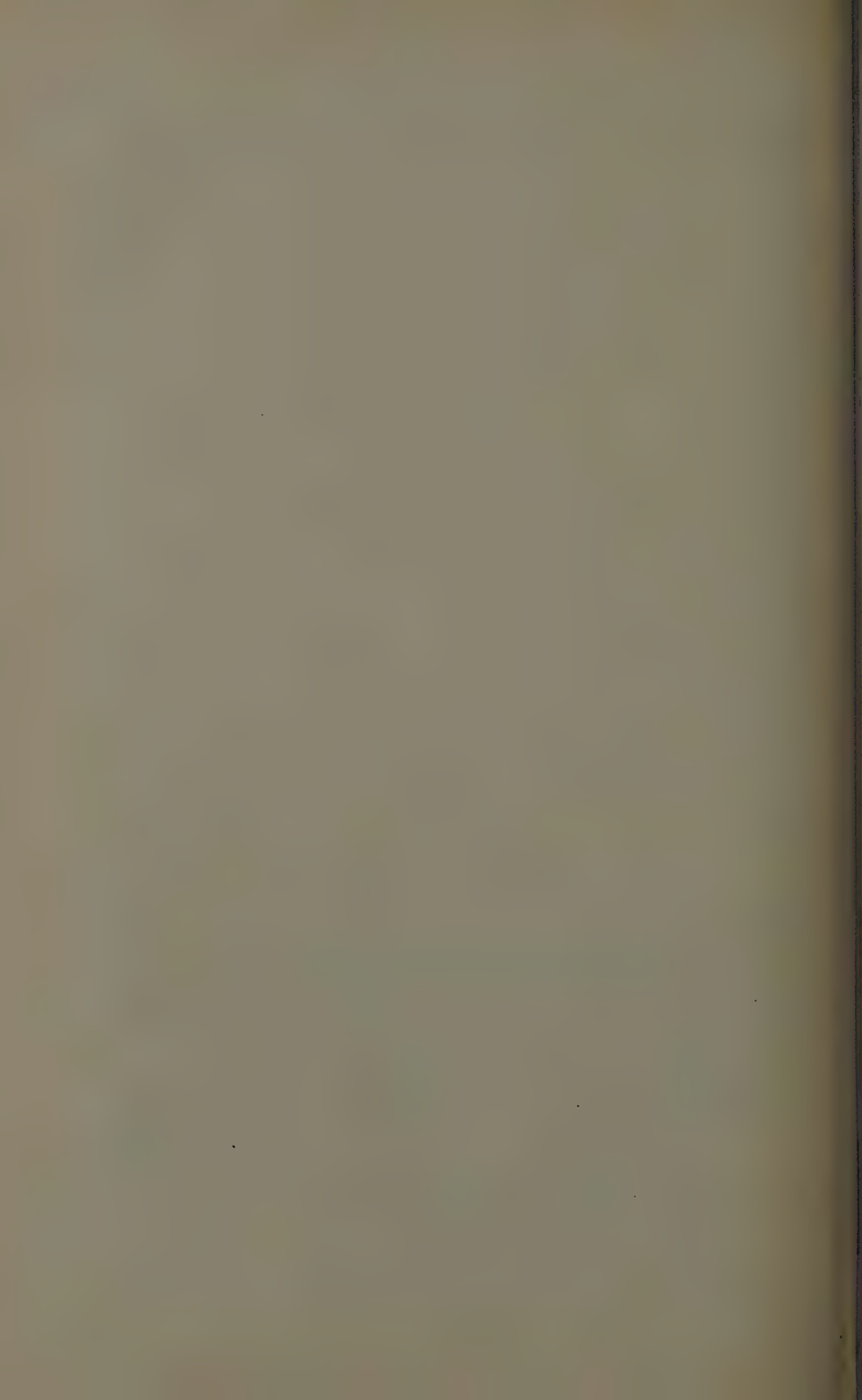
C: 15 cm. off ground among dense millet (pl. 7, fig. 14); wind speed at 14.00, 0.7 m./sec.

D: 5 mm. off ground on small bare patch among dense millet (pl. 8, fig. 15); wind speed (5 cm. off ground) at 14.00, 0.5 m./sec.

D₁: 5 mm. off bare ground, lee side of clearing among millet (pl. 8, fig. 16); wind speed (5 cm. off ground) at 14.00, 0.1 m./sec.

E: 5 mm. off bare sand of exposed dune outside millet (as pl. 2, fig. 3, or pl. 3, fig. 4); wind speed 5 cm. off ground at 14.00, 4 m./sec.

Wind speeds and directions 1.5 m. over exposed dune outside millet: 06.55, N, 1 m./sec.; 08.20, ESE, 2.5 m./sec.; 10.15, ENE, 3.7 m./sec.; 14.00, E, 5.5 m./sec.; 16.15, E, 5.2 m./sec.; 17.45, E, 5.0 m./sec.; 18.30, N, 1.5 m./sec.



direction and strength in the upper air cannot be judged from conditions close to the ground. With vigorous flight and moderate wind considerable deviation from wind direction is conceivable and has been recorded by Lépiney (1928). There seem grounds for supposing most flight directions to be less than 90° each side of the downwind direction, and a considerable majority within 45° each side of it.

The prevailing wind during the winter breeding season on the Sudanese coast carries the majority of immigrants away from the outbreak centres in a direction in the south-west quadrant. Large tracts of the coastal plain, between the "Suaeda belt" of Maxwell-Darling (1936) containing the outbreak centres and the hills, are always bare, and alighting locusts would be more inclined to take-off and continue flying, even in daytime, in response to hunger or high midday temperature, and in the absence of visual attractants or perches off the ground, than in the better-covered zones of the Suaeda belt. Farther to the south-west is the range of Red Sea Hills with green vegetation even in summer, still farther inland the rains fall in summer instead of winter.

In view of visual attraction in flying locusts, it would be rash to reject the theory of attraction from the air to conspicuous patches of green vegetation in otherwise barren country of contrasting colour.

The possibility arises then that locusts flying out along roughly the same course, and descending to the first conspicuous areas of green vegetation encountered, may re-concentrate to some extent in these areas.

The coastal outbreak centres could be re-populated in their turn from the inland centres with the aid of the strong south wind of summer and autumn. Emigrants leaving at this time would also be carried to the Arabian coastal breeding areas (Maxwell-Darling, 1937) and might be brought back in winter.

Now that evidence of solitary migration has been found in three permanent reserves of *Schistocerca*, Baluchistan, the Mauritanian and Sudanese coasts, a centre such as Hamashiameb cannot necessarily be complete as an outbreak centre. In fact, the Sudanese part of the Red Sea coast is not proved the point of origination of serious outbreaks, although it may be so. It is known that incipient swarming occurs, and ready-made swarms are able to multiply there prior to further flights. I suggest that this coast is part of a complex of centres, and the rest may be in the Eritrean or Sudanese hills, still uninvestigated, or the Arabian coast of the Red Sea (Maxwell-Darling, 1937), just as the coastal and inland area of Mekran are complementary centres for Indian outbreaks, and coastal and inland areas possibly complementary in Mauritania.

A possible means of preventing flying swarms settling on cultivation is also suggested by the above considerations.

Smoke from smudge fires or special powders has been suggested, and used, as an irritant to ward off flying swarms. The observations described and cited in this paper (pp. 427-434, 447-449) on visual attraction to dark conspicuous objects suggest that this may be responsible for swarms settling on cultivation, especially in barren country.

Light-coloured smoke is suggested therefore not as an irritant but as camouflage; if a cultivated area could be made to appear no darker from the air than does the surrounding country a swarm might not descend on it.

4. Discussion of concentration.

Incomplete as the results of observations on movements and concentration recorded here may be, there are few published accounts with which to compare.

Where comparison is possible in particular connections it has been made in the relevant passages.

Disagreement with Maxwell-Darling's (1936) suggestion that *H. undulatum* is an important concentrating factor owing to hoppers' preference for it as food has been expressed. It is interesting that despite his conclusion, he found that young hoppers at Arbaat in January 1934 concentrated on "the greenest patches of *annuals*" [my italics] showing that concentration may occur without *H. undulatum*. His hypothesis, moreover, does not assist in explaining concentration in relation to large areas of zone III where *H. undulatum* was scarce. Maxwell-Darling mentions the "braking" effect of thick undergrowth on marching bands of *gregarians* hoppers. An interesting note is that of Grassé (1923), who found that the tendency of *Anacridium aegyptium* L. to move to light could be overcome if a surface on which it could climb were encountered. Uvarov (1921), Smee (1936) and others also mention the braking effect of vegetation on gregarious bands. In regions where vegetation is better developed than on the Sudanese coast, as is usual in outbreak centres of locusts other than *Schistocerca*, the braking effect is probably less important in concentration.

Maxwell-Darling (*loc. cit.*) and Predtechensky (1935) mention the relative inactivity of young non-gregarious hoppers of *Schistocerca*. Edney (1937) in laboratory experiments on *Locusta* found older, solitary hoppers more active than young hoppers or adults. My observations on *Schistocerca* agree with this, but Zolotarevsky (1933, 1938) considers adults of *Locusta* the most active stage, and that hoppers in general stay near their hatching sites.

Sviridenko (1924) and others note the tendency of gregarious locusts to disperse after the final moult. Uvarov (1928) considered this indicated a "lowering of the gregarious impulses," but as it is also found among solitary adults it may be that adults by their power of flight have a wider range of movement and it is relatively easy for them to scatter.

Concentration on the small scale studied at Hamashiameb was scarcely touched on by Ramchandra Rao (1937b, *et ante*) and his co-workers on *Schistocerca*, other than to mention that incipient bands and swarms seem associated with millet cultivation. A few cases (St. Clair, 1930; Faure, 1934; Maxwell-Darling, 1934) of local concentration movements by *Schistocerca* to fresh vegetation are suspected but proof is wanting.

For ACRIDIDAE in general, other than *Schistocerca*, conditions are so different that comparison is of little value. Much work on distribution on a large scale has been done, correlating presence or absence of locusts with vegetational and climatic factors, largely to delimit the "permanent reserves" and outbreak centres. Reviews of this subject appear in Appendices 7 and 27 of the Proceedings of the 4th International Locust Conference (1937).

Concentration within an outbreak centre, where it has been studied, is usually correlated with patchy drying up of vegetation or variable flooding, with no analysis of the mode of operation of these factors.

Zolotarevsky (1933) observed the distribution and movement of hoppers of *L. migratoria capito* in Madagascar, in relation to humidity, and he attributed control of concentration movements to humidity reactions. His recent studies (1938) on *migratorioides* in French Sudan are claimed to support this view. Patchy drying of vegetation is a common feature of outbreak centres, including those of *Schistocerca*, and its importance in concentration is undoubted so that Zolotarevsky's statements deserve attention.

Figures given by him in support of his contention are not large (see p. 482).

In the laboratory I found 1937 *migratorioides* showed consistent negative hygrotaxis which brought it to the lowest relative humidity available, even in starved individuals in low humidities. In concentration in nature, only hygrokinesis is likely to be effective, but the hygrokinetic reaction of *Locusta* would cause collection in the driest situation available, although not strongly. When wind is blowing, moistened air from a patch of green vegetation will be carried downwind, and the humidity gradient be gentle and disturbed by turbulence, so that hygrotactic reactions could not assist in concentration, but a positive hygrokinetic response, as exists in *Locusta*, with the directed reaction to wind existing in *Schistocerca*, would assist in concentrating locusts downwind of a concentration patch. These seem the only circumstances in which humidity could play some part in directing movement to a concentration zone. Moreover, if positive hygrokinetic reaction persisted after arrival in the zone, other reactions would be required to prevent the insects leaving. In *Schistocerca* such combined response to the activating effect of humidity and the directing effect of wind, is not proved or disproved, but as wind on the Sudanese coast is fairly constant this response might assist concentration only in a minority of cases. Other factors have been suggested as decisive. Zolotarevsky (1938) wrote: "Ces constatations prouvent que les limites de l'hygro-preferendum de l'espèce en sa phase grégaire indiquées par O. B. Lean (1931), considérées dans le cadre du micro-climat, sont applicables aux insectes menant la vie solitaire et sédentaire." Nevertheless, neither dependence of sexual maturation, correlation of movements with drying out of vegetation, nor correlation of swarm distribution with humidity (Lean, 1931) comprising the "constatations" of Zolotarevsky, may be said to prove a "hygro-preferendum." Preference for food with adequate water content, or non-survival or absence of breeding in dry atmosphere could affect distribution, but "hygro-preferendum" is another matter and remains to be proved.

Some hesitation in accepting Zolotarevsky's conclusions seem therefore inevitable. Reaction to relative humidity may play a part but further study is necessary before it can be called paramount.

My observations may perhaps be related more profitably to the respective rôles of Real and Virtual Concentration in outbreak production.

Zolotarevsky (1929, 1933) drew up a well-documented scheme of the stages of an outbreak on the basis of his observations on *L. migratoria capito* in Madagascar, and Uvarov (1932) a similar scheme for *D. maroccanus* in western Anatolia. In this scheme an initial period with ample rain and generally favourable conditions allows a great increase in numbers of locusts in the outbreak area, followed by an abnormally dry season when locusts collect in and around the areas with fresh vegetation, and oviposit there, causing crowding in the next generation. This theory involves the combined effects of Real and Virtual Concentration. Zolotarevsky (1937) and Uvarov (1937) have reaffirmed the opinion that this is so for locusts in general; my observations on *Schistocerca* support it. Without Real Concentration (particularly in the 1st generation), the Virtual Concentration of the 2nd generation would be less intense. Without Virtual Concentration of the 2nd generation, Real Concentration would be inadequate to produce an outbreak.

Instability of climate, and of vegetation zones, is a feature of outbreak areas in general, and, as Zolotarevsky and others point out, its significance is that while favourable conditions are required to increase population density (Virtual Concentration) this density would not increase further, and might decrease, unless an unfavourable period ensued when concentration zones shrink in size,

the locusts deserting the rest of the area (Real Concentration) perhaps to undergo further Virtual Concentration in the restricted patches. Therefore Zolotarevsky correlates outbreaks with periods of drought after heavy and prolonged rain. Pasquier (1934) found seasonal rainfall fluctuated little in the outbreak area of *D. maroccanus* in Algeria and concluded that favourable conditions of rainfall alone, without subsequent drought, could produce an outbreak, thus emphasising Virtual Concentration.

Without accepting this, and agreeing with Zolotarevsky's scheme as applied to *Schistocerca* on the Sudanese coast, greater emphasis should be laid on Virtual Concentration. On this coast a shrinkage of vegetation zones is normal every spring, and Real Concentration follows. Conditions in an outbreak centre between one rainy season and the next are such that few locusts survive and these are scattered, so it is difficult to regard an outbreak as built up *within Hamashiameb* (but see p. 459) over several seasons, as suggested for other locust outbreak centres (Lean, 1936; Faure, 1937; Zolotarevsky and Murat, 1938; Zolotarevsky, 1938). That the decisive factor in an outbreak year is the unusual amount and duration of rainfall, permitting the production of a 2nd generation and a high degree of Virtual Concentration, is clear from Maxwell-Darling's and my observations. It appears that Virtual Concentration is probably also the decisive factor in the Mauritanian outbreak centres of *Schistocerca* (Zolotarevsky and Murat, *loc. cit.*).

In outbreak centres of *L. m. migratorioides* in the middle reaches of the river Niger (Lean, 1936) Real Concentration seems connected with invasion of concentration zones by the annual rising of water. Lean considers that the abnormally low floods of 1926-1927 which permitted extensive and uninterrupted breeding (Virtual Concentration) was the decisive factor for the subsequent outbreak. The Real Concentration produced by the rising water was important only because Virtual Concentration had gone so far. Zolotarevsky (1938) considers this account over-simplified but for present purposes the principles are unaffected. While conditions are completely different from the Sudanese coast, the principles of outbreak production seem analogous; in both cases Real Concentration is not especially associated with outbreak years, and Virtual Concentration due to extensive breeding is the decisive factor.

Insufficient is known to form an opinion on the relative importance of the two types of concentration in the outbreak areas of *Nomadacris* (Micheltore, 1937), but variable flooding is also a feature of these areas.

The operation of similar principles (the decisive rôle of Virtual Concentration) is suspected in outbreak centres of *L. migratoria migratoria* and *rossica* in the Soviet Union and *manilensis* in China despite differences in vegetation and other conditions (Uvarov, 1921, 1928, 1936; Predtechensky, 1928).

I consider that Real Concentration is more important in the centres of *L. migratoria manilensis* in the Philippines, Borneo and Malaya (Uvarov, 1936), *L. m. capito* in Madagascar (Zolotarevsky, 1933) and *Locustana pardalina* in South Africa (Faure, 1937). In the outbreak area of *L. m. capito* on which Zolotarevsky based his original theory, shrinkage required an unusually dry year, so that an outbreak involves the combination of good rainfall for Virtual Concentration with subsequent drought for Real Concentration, the latter being decisive.

The difference is only of emphasis but may be of practical interest in the analysis and forecasting of outbreaks.

5. Summary.

1. Adults surviving the summer oviposit in the course of the flood near the previous year's cultivation, but sometimes up to 100 m. from the dunes or current year's cultivation.

2. Food preferences appear to play no great part in subsequent distribution.

3. Young hoppers remain in the first vegetation encountered (*H. undulatum* mats on the dunes, grass or *H. pallens* elsewhere).

4. Older hoppers wander at a rate varying with density of cover, reaching a maximum of 100 m. per day on the bare plain. Variations in wandering rate assist concentration into zones of densest vegetation, preferably with bare patches interspersed.

5. For short distances hoppers are visually attracted to, and trapped in, conspicuous vegetation regardless of undergrowth density.

6. As a result of 4 and 5, concentrations of some older hoppers appear in millet, or similar vegetation, visual attraction being the main cause.

7. Concentration of hoppers from all directions to a given point seems impossible from more than 30 to 50 m.

8. Ensuing adults remain at first in the same zones but, after hardening, scatter from local plots outside cultivation. They are less affected by density of ground vegetation, spreading throughout millet regardless of the presence or absence of weeds.

9. The normal range of movement of undisturbed adults is less than that of older hoppers and difference in wandering rates between zones plays little part in adult concentration, but the frequent disturbances cause short flights to be made and increase range of movement.

10. Adults are susceptible to visual attraction to conspicuous vegetation, this being apparently the sole positive factor in their concentration.

11. Spontaneous taking-off followed by sustained flight is possible, but its frequent occurrence is not proven, and it appears unlikely to assist local concentration in the outbreak centre.

12. Weeding and local drying of vegetation contribute to concentration of hoppers and adults.

13. The above aspects of concentration involving active movements are classified as "Real Concentration."

14. With a 2nd winter generation (not produced at Hamashiameb in 1937) members of it would start life in a concentration zone, and remain trapped so that increase of individuals would increase crowding greatly. Such concentration resulting from localised breeding is termed "Virtual Concentration."

15. The degree of Real Concentration achieved by the 1st generation seems necessary but inadequate to produce an outbreak. Virtual Concentration of a 2nd generation, dependent on ample and prolonged rain, appears decisive in producing an outbreak.

16. It is possible that the Sudanese coastal centres do not constitute a complete outbreak area, but are part of a larger complex, between one and another part of which solitary migrations occur.

B. AGGREGATION

Aggregation, it will be recalled (p. 406), refers to the possibility of frequent encounters between hoppers or adults where present in large numbers, assuming such encounters to be essential for "Gregarisation." The maximum of older

hoppers recorded in a concentration zone was about 10 per sq. m. Even where the true figures were greater, if the locusts were always as inactive and "phytophilous" as the young *congregans* hoppers observed by Maxwell-Darling (1936), opportunities for aggregation leading to gregarisation seem few. The comparatively isolated life of such hoppers in dense vegetation, despite high population density, is stressed by Maxwell-Darling (*loc. cit.*).

However, even in such circumstances aggregation can occur. A mass of hoppers on an *H. undulatum* mat (pl. 3, fig. 4) or elsewhere adjacent to bare ground (pl. 8, fig. 16) can be forced, by disturbance, to leave the vegetation in large numbers, as Maxwell-Darling (*loc. cit.*) and I have observed. Once on bare ground, a hopper is subjected to intense visual and mechanical stimulation from its fellows in the few moments before returning to vegetation. Similar short aggregation conditions were undergone by adults when numerous in a concentration zone, for as man or beast moved in the cultivation, locusts flew up as many as 50 at a time to settle again in a few minutes.

It is impossible to gauge the efficacy of such brief experiences of aggregation in producing gregarisation. It seems doubtful if it is adequate to complete it.

Opportunities for "spontaneous" aggregation were sought, and found.

"Spontaneous" aggregation is not easily observed since movement by the observer may disturb the locusts. Realisation of its occurrence in the absence of disturbance was accidentally made when the interior of unweeded millet was observed from the back of a camel outside cultivation. Many hoppers were visible, not on weeds or millet stands, but in groups on small patches of bare ground (pl. 8, fig. 15). Subsequently, similar group formation on bare sheltered sunlit ground was often observed. It was most marked in 4th and 5th stage hoppers, but evident among 2nd and 3rd stage hoppers and adults. The name of "groups" is given to these collections since, as it is hoped to show, group formation is unconnected with the "gregarious instinct" keeping bands and swarms of *gregaria* together.

1. Diurnal behaviour of older hoppers in unweeded millet.

The diurnal behaviour regime varied considerably according to vegetation zone and age of the locust. Older hoppers, 4th and 5th instars, were present longer than other stages at Hamashiameb and were most numerous in unweeded millet. Most observations were made on them, and in this zone, and the behaviour of other stages, and in other zones, may be compared subsequently.

Hoppers spend the night in a mildly torpid state on the millet stands, mostly near the top. Even at dawn they are not easily disturbed, dropping to the ground rather than moving out of sight on the same stem as they do in the day. At sunrise, or soon after, the first spontaneous movements are made. In the next 30 to 60 minutes hoppers climb to the top of the millet stands, many exposing themselves broadside to the rising sun. Feeding begins about this time, continuing during the next hour or two and hoppers become more active. Some descend, others ascend, the stands at different levels. Behaviour is rather indefinite but finally most are found on bare sunlit patches of ground. Where population density is high loose groups are formed on such patches, but where it is low hoppers are found in ones and twos on any bare, sheltered and sunlit ground.

Close observation showed that while a group may remain in a place for several hours, its composition slowly changes. When a hopper comes to the

bare ground from surrounding undergrowth or a millet stand, it takes a position in the sun. After a little fidgeting it usually comes to rest after a few minutes. In a minority of cases the body is orientated perpendicular to the sun's rays. It rests on the ground with hind legs folded and nearly flat on the ground; the antennae often lowered over the face. Its general appearance resembles sleep, but it is no more asleep than other animals basking in the sun; it responds immediately to stimulus. Even the arrival or departure of another hopper may cause the raising of the antennae and hind legs or even locomotion, and such disturbance as the arrival of a bird or man causes immediate removal to the shelter of vegetation. Thus the quiescence of a basking hopper is not "heat stupor." Slight movement of legs or antennae is made in the absence of apparent external stimuli, an undisturbed hopper raising its antennae, then hind legs and body, leaving the group and wandering off into vegetation after about half an hour. This figure is very rough, only few hoppers being timed. In spite of departures the groups persist, as new arrivals continue so long as external conditions remain constant.

Hoppers on vegetation feed at all times, but as most are basking, feeding is less intense in the day than the morning or evening.

On cloudy days, in the majority in January and February, basking persists throughout the day, but not in the same places. As the sun moves and shadow creeps across the basking patch, those first in the shade stir, and after a few minutes, leave the patch or come to rest in a place still in the sun. When the patch is quite shaded all hoppers have left and groups appear in new positions previously shaded but now sunny.

When the sky is cloudless and screen temperatures rise to 30° C. or over (an unusual event before the second half of March) basking does not persist in the hottest part of the day. Before midday departures become frequent, and new arrivals do not stay long. Soon all groups are broken up and hoppers scattered, some in the shade on the ground, some in the shade on millet stands, most higher up the stands in the sun, but all in cooler places than those vacated. In the hot time of day, sunny bare ground is avoided by all but an occasional hopper, which, on coming to ground, runs rapidly, or hops, into shade or on to a perch off the ground.

After midday as the temperature falls the groups re-form. As the afternoon progresses less ground in the cultivation is reached by the sun and groups become fewer and larger. More hoppers are found on the millet stands, especially in sunny positions. As the sun sinks the shade rises on the stands and hoppers are found at higher levels. Feeding becomes general again. Hoppers do not keep to the lowest levels penetrated by the sun, but climb above it. Where ground is lit by the sun till sunset hoppers bask until half an hour before sunset, when they also climb. By sunset no hoppers are found on the ground and few, except as mentioned later, in the undergrowth. The majority are on the upper third of the millet stands. Crawling and feeding may continue after sunset, especially after a warm day, but when the first stars appear movement has virtually ceased. Hoppers are hanging on stalks, leaves and heads, usually with head facing upwards. For a short time they are sensitive to disturbance but soon become semi-torpid. The daily routine of older hoppers in unweeded millet may thus be summarised :—

1. Beginning of activity.
2. Morning ascent and exposure of bodies to sun.
3. Morning descent to ground.
4. Basking on bare ground, in groups if numerous.

5. Midday break up of groups, scattering to cooler positions and climbing millet stands.
6. Afternoon descent, resumption of basking and re-formation of groups.
7. Evening break-up of groups and ascent of stands.
8. End of activity.

2. *Correlation of diurnal behaviour with micro-climates.*

When a well-defined diurnal regime was discovered in solitary locusts, investigation of some factors producing and controlling the regime was made.

On the basis of previous knowledge six or eight positions were selected at various heights on the millet stands, on top of undergrowth, on patches of bare ground, etc., known to be available to and frequented by locusts in their diurnal regime. Instruments were arranged in each position before sunrise. Throughout the day readings in all positions were taken at intervals of half an hour and continuous notes made by another observer on behaviour in the vicinity. Half-hourly readings were as much as could be managed, for a round took 10-20 minutes. The sets of instruments were always read in the same order but simultaneity was impossible and this sometimes introduced errors due to the passage of cloud over the sun.

Readings less frequently than half-hourly were undesirable because of rapid changes in conditions, and instruments needing more than a few seconds to read could not be used. Difficulty was found in the selection of suitably "representative" positions; no position, for instance, on the ground in dense millet remained unshaded throughout the day, but the locusts, by moving, spent most of the day in unshaded positions. It was necessary, therefore, sometimes to move instruments at midday from a place sunny in the morning to a place sunny in the afternoon.

(i) *Temperatures.*

a. "Sun," Air and Soil temperatures.

Temperature of the surface and interior of the body is affected by that of the surrounding air and by radiation, from the sun or re-emitted from objects. Radiant heat is important, since locusts spend most of the day in exposed positions. No instrument recording intensity of radiation separated from temperature of the surrounding air was available. Ordinary thermometers absorb some radiant energy and give a higher reading in sun than in shade, but this is only an indication of radiation effects. As the thermometer bulb is not affected by conduction, convection, and radiation in the same way as is the body of a locust, the temperature of the latter cannot be estimated from reading the former. This can only be done by calibrating the difference in body temperature and the surrounding air temperature, in terms of differences in reading of a thermometer and surrounding air temperature. Unfortunately air temperature is difficult to measure especially in the tropics, when it is undesirable to stir the air, as in bare patches among millet. The Whirling Hygrometer or Assmann Psychrometer could not therefore be used to record air temperature or relative humidity, and a stationary thermometer bulb is affected by radiation even in the shade.

In the absence of other methods, ordinary uncoated thermometers with bulbs 17 mm. long and 3 mm. in diameter were incorporated in each set of instruments. Each thermometer was horizontally fixed to the roof of a small shade (see below, and pl. 6, fig. 11; pl. 7, figs. 13-14) with the bulb projecting

free of the wooden surface. On the ground, the "sun thermometer" was laid on the sand, its bulb 5–10 mm. off the surface. The thermometers were all moved at intervals, their long axes kept roughly perpendicular to the sun's rays.

To indicate air temperature similar thin-bulbed thermometers were fixed with their bulbs under small wooden shades (pl. 7, figs. 13–14; pl. 8, fig. 16). The shades had a sloping roof, a floor, and narrower walls in front and behind. The bulb of the shade thermometer almost touched the top of an Edney Paper Hygrometer suspended under the shade. On the ground the shade was from a piece of rush matting on two short pieces of wood lying on the ground and supporting the thermometer and hygrometer (pl. 8, figs. 15–16). The shades were rotated at intervals during the day to keep the instruments out of the sun.

The reading of the shade thermometer was higher, even in wind, than that of the Assmann Psychrometer, by as much as 1–2° C. In sheltered ground positions differences were sometimes more than 2° C., but allowance should be made for cooler air drawn into the Assmann from levels above that of the shade thermometer. Several types of small shades, covered with aluminium foil, were tested but showed no improvement on the wooden shade, suggesting that the error was due to re-emitted radiation entering from the sides. On the ground, however, not only the Assmann but also a thermometer under a perfect reflector would not give true air temperature, since the soil as well as the thermometer is shaded, and thus heats the air less than exposed soil would do. The data obtained from the small screens was thus of less value than had been hoped, but they are of little interest in relation to locust behaviour, for these remained most of the day in the sun.

The only measure of temperature usually available therefore was the indirect and complex one given by an uncoated thermometer bulb in the sun. Some correlation between these readings and behaviour was nevertheless found.

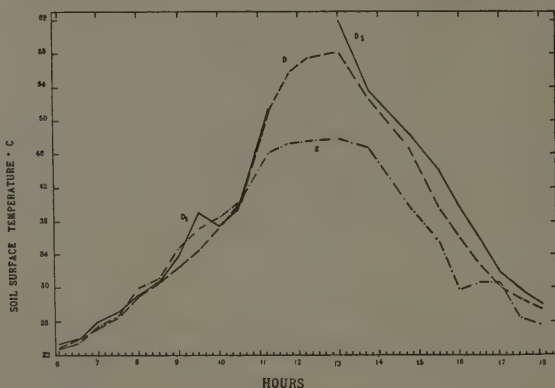
Temperature and humidity readings for complete days with parallel records of movements were made as follows: twice on mats of *H. undulatum* with indigenous hoppers of all stages; twice in unweeded millet with all stages of indigenous hoppers and adults; once in clean millet with *dissocians* hoppers in small bands, isolated green *dissocians* hoppers and adults; and twice in clean millet with *dissocians* adults only. Supplementary shorter observations were also made.

The observation on indigenous hoppers in unweeded millet made on 16.ii. was more satisfactory than that on 12.ii., not only because the position was more representative and the radiation less variable, but because it was an exceptionally hot day when midday behaviour showed the special features described above. Therefore the data for 16.ii. are given in figs. 10, 11, and 12; the weather, however, was abnormal and the peculiar midday behaviour did not occur normally when indigenous hoppers were present at Hamashiameb. Fig. 10 shows "sun temperatures" on 16.ii., with behaviour of hoppers and adults; fig. 11, the soil surface temperatures in the ground positions on the same day.

After a minimum temperature of 22° C. in the standard screen the previous night, activity began at about 23° C. soon after sunrise at 06.05 hours. Temperature differences were small. The morning ascent began at once and by its end most hoppers were feeding or vertical in the sun. The difference in sun and air temperature in the millet heads (A in pl. 11) was about 1° C. The ill-defined movements which followed and ended with most hoppers on the ground (morning descent) lasted some 80 minutes. Positions on the ground had then

been warmed 2° or 3° C. higher than on the millet. The bare sand outside cultivation warmed most rapidly, but, as the wind rose, sheltered ground positions in cultivation became warmer than E outside. Between 08.00 and 11.00 hours most hoppers appeared to be on bare ground such as D and D_1 . Hoppers did not bask more than 10 or 20 cm. from ground vegetation. On larger bare patches (pl. 8, fig. 16) they kept to the edges (D_1).

During morning basking when many groups were formed, temperature differences increased to as much as 10° C. more on the ground in the sun than among the millet heads. At 11.00 the temperature of the warmest basking-place had risen to well over 40° C.; the groups broke up, and most hoppers climbed the millet stands. They reached levels (B) where the sun temperature was several degrees below that of the basking positions when groups were there. Most hoppers remained on the millet till 14.15 hours, but some descended again at



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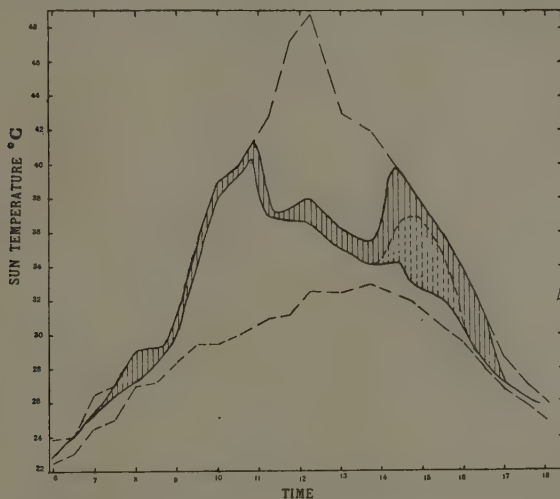
FIG. 11.—Readings of thermometers on the ground with their bulbs just covered by sand, in positions D, D_1 and E (see fig. 10) on 16.ii.

13.40, moving up the temperature gradient from 35° to 36° C. to about 40° to 41° C.

From 14.30 to 16.30 basking with group formation was resumed. The size and number of groups was less than in the morning; possibly the reduction was due to the ground sloping eastwards, and less ground was left unshaded in the millet when the sun moved into the western sky. Reduction in size requires another explanation, and as it was often observed, it is thought probable that less hoppers descended in the afternoon than in the morning. It may be that having lost a certain amount of water in the morning, more hoppers fed in the afternoon. Groups enlarged as the number of bare sunlit patches decreased later in the afternoon. During afternoon basking many ground positions remained warmer than the millet, especially if, like D_1 , they were not shaded until within an hour of sunset; thermometers still showed higher readings than those on millet, yet at 16.00 hours the evening ascent began and continued after sunset. Before sunset bodies of the hoppers were perhaps warmer on the millet than in the shade since they absorb solar radiation better than do thermometers, but after sunset the ascent continued, when hoppers were certainly warmer near

the ground. Thus the evening ascent took place before the "inversion of temperature," and movement was sometimes down a gentle air temperature gradient. Many places were shaded before 16.00 and the temperature must have fallen almost as low as that in the sun.

Fig. 12 is based on fig. 10; the warmest temperatures (on the ground) are shown by the upper broken line (omitting E outside the millet), and those of the coolest place (A) in the millet heads, by the lower broken line. The space between the lines represents the available range of temperature in the millet during the day. Using the curves of fig. 10, the temperature where most hoppers were found at successive periods, was entered giving the outlines of the shaded area on fig. 12, which provides a rough indication of the temperature range occupied by the hoppers.



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FIG. 12.—Distribution of older hoppers in relation to the range of available "sun temperatures" on 16.ii., based on fig. 10. Broken lines indicate the temperatures at the warmest and coolest of the selected positions, and the shaded area the range of temperatures occupied by the hoppers, throughout the day.

The close relation of hopper distribution to temperature is made clear by fig. 12. At first, with a narrow temperature range they were not in the warmest positions. During the morning descent the range occupied by the hoppers was wide and almost covered the range available, but as the descent drew to a close they were confined to a narrow zone at the upper limit of the available range. They remained there till the thermometers read 40–41° C., when the groups broke up rapidly and hoppers climbed the stands to occupy a wider range of temperatures at a lower temperature level. When ground temperature again fell to 40° to 39° C. groups again appeared at the warmest places. Since much ground became shaded and many hoppers remained on the plants after the midday ascent, the range of temperature occupied during afternoon was wide and included the less heavily shaded parts of fig. 12. In bare sunlit patches, however, restriction to a narrow range at the upper limit available was

again noticed. Later the range occupied widened again as the general evening ascent proceeded and then most hoppers were not in the warmest available places, which were still on the ground.

Fig. 13 is based on observations made on 12.ii. and constructed in the same way as fig. 12. This was a typical February day (16.ii. was not), sun temperature on the ground never reaching $40^{\circ}\text{C}.$, and the majority of hoppers remained close to the upper limit of temperature range for most of the day, basking on the ground. Similar behaviour of extreme *dissocians* 5th instar hoppers is shown in figs. 35 and 36 and described on p. 522.

As stated already, the evening ascent often occurred in the absence of, or down, a slight temperature gradient. Sometimes a different behaviour in which temperature appeared to play a greater part was noticed instead of the normal evening ascent. Close to the instruments used on 16.ii. was a bi-metal thermograph under a matting screen such as is shown on pl. 5, figs. 9 and 10.

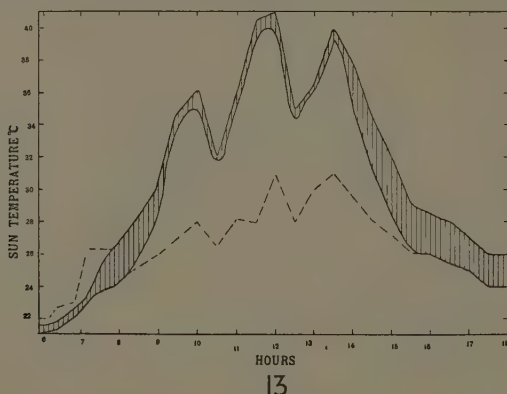


FIG. 13.—Distribution of older hoppers in relation to the range of available "sun temperatures" on a normal day in February (12th). Constructed in the same manner as fig. 12.

These screens, almost enveloping the instrument, kept it free of dust but rendered it useless as an indicator of free air temperature. Hoppers and adults took advantage of the micro-climate created by the screen. Temperature under the screen, having been lower than in the sun on the ground during the day, did not fall so rapidly and at sunset was still as high as on ground recently left by the sun. The screen was in shade much of the afternoon and the air around it must have been lower than at positions D and D¹. Over 20 hoppers and adults were found under the screen after sunset when all others in the vicinity were high up on the millet. This was also observed on other occasions when the difference in air temperature inside and outside the screen was about $2^{\circ}\text{C}.$

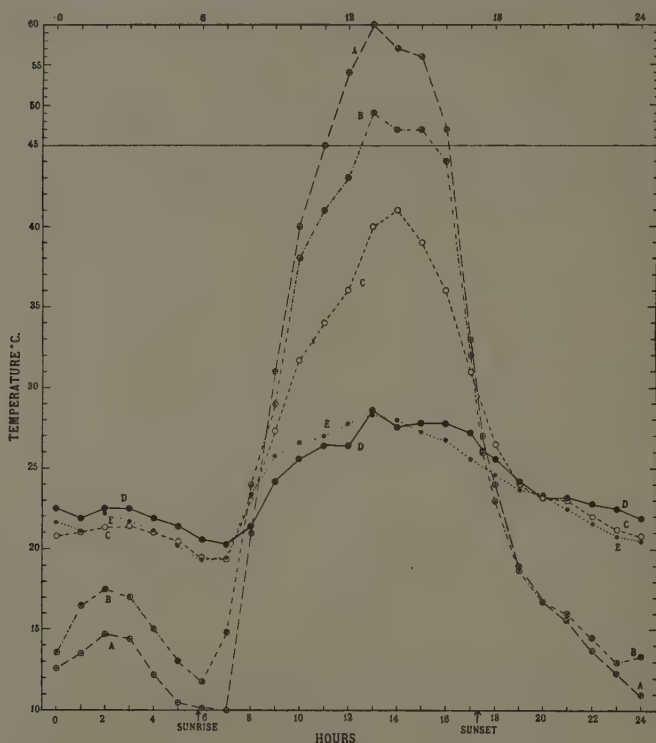
A similar observation was also made under more natural conditions. Where the observations on 12.ii. were made, there was much dense grass in the millet and along its southern border, and large *Suaeda* bushes up to 2 m. in height and diameter. Temperatures were recorded at the bottom of dense grass 40 cm. deep but the patch of grass chosen was shaded from soon after midday, and at sunset temperature below it was no higher than on top of it and lower than

on bare ground in the sun. In less deep grass on the edges or away from millet and exposed to afternoon sun, temperature at the bottom was up to 2° C. higher than on the top at sunset. At this time, some locusts were found down in the grass. The tendency to descend and remain at the bottom of the grass was noticed also in the half-hour wandering experiments. Locusts also collected at sunset in the large *Suaeda* bushes, where again it was 1 or 2° C. warmer than outside.

These observations are of interest with regard to the effect of the evening "inversion of temperatures" on behaviour. On bare unsheltered ground the inversion undoubtedly occurs. In fig. 10, the line E (bare exposed dune surface) crosses and falls below the standard screen line (also over bare ground) just before sunset and there is already 1° of difference between the two positions less than an hour after sunset. On the other hand, whenever ground is "blanketed" by vegetation an alteration of circumstances of inversion was to be expected. Fig. 14, in conjunction with the readings of ordinary thermometers (see above), will help to illustrate these points, although imperfectly. Curves D and E, the records of bi-metal thermographs, a metre above the ground in the middle of a bush 2 m. by 2 m., among millet, and in the standard screen respectively, are the only lines giving a true record of air temperature in their positions. The other three lines are records from mercury-in-steel distance thermographs. Curve C is the temperature of such an element close to the ground under dense grass 20 cm. deep, and the reading was as much as 5-6° C. over the temperature of the air given by an ordinary thermometer in the same position at midday. However, at and after sunset it agreed with a thermometer. The other two elements were unshaded and showed as much as 20° C. in excess of ordinary thermometers in the day and much below at night. At sunset, however, they agreed with ordinary thermometers, and while the readings cannot be compared with shaded instruments the relation between the two gives a sufficiently accurate picture of the inversion taking place between the two positions. One of them (A) was 1 cm. above the bare sand of a sheltered basking-place, and another (B) was 30 cm. above A. Readings of a mercury-in-steel element set level with the top of the grass over B are not shown in fig. 14, but they followed curve B closely.

Allowing for differences in exposure of the instruments the following conclusions may be drawn from fig. 14. During the day, temperatures under the grass and in the *Suaeda* bush are lower than in positions exposed to the sun. At about sunset temperatures in exposed positions fall rapidly, but as they fall more slowly in "blanketed" positions, there is little difference in shaded and unshaded positions at this time. After sunset temperature of the air and of solid objects (including locusts) losing heat by radiation, fall below temperatures in sheltered positions. This is an inversion of temperature opposite to that over bare unsheltered ground. Readings of the steel elements in fig. 14 exaggerate the inversion occurring between air temperatures (or locust bodies) in the two positions, but ordinary thermometers also show this inversion, and the body of an exposed locust cools to slightly below the temperature of the surrounding air (see below). Between the position under grass and in the *Suaeda* bush there is a slight inversion in the same sense, perhaps because of the greater evaporation from grass than from the salt-bush. Between the two exposed positions over bare sheltered ground the inversion occurs in the same sense as that over bare unsheltered ground, but the degree is small and it is delayed until 2 or 3 hours after sunset. Thus a "reversed inversion" associated with well "blanketed" ground occurs soon enough and to sufficient

degree to affect behaviour. On the other hand, normal inversion over bare ground is so delayed and diminished when the ground is surrounded by vegetation that its effect is small on locusts, which have already ceased activity.



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FIG. 14.—Hourly readings of five thermographs in various positions and exposures during 27.ii., illustrating "temperature inversion." Temperature scale contracted at top.

- A: Unshaded mercury-in-steel element of a distance thermograph, 1 cm. off the bare sheltered ground of a "basking-place."
- B: Unshaded mercury-in-steel element of a distance thermograph, 30 cm. over the element of A.
- C: Mercury-in-steel element of a distance thermograph 1 cm. off the ground under dense, 20-cm.-high grass.
- D: Bi-metal thermograph 1 cm. off the ground in the middle of and completely shaded by a large *Suaeda* bush among millet.
- E: Bi-metal thermograph in the standard screen at the camp.

The readings of the different instruments cannot be compared directly. For further explanation see text.

This applies only to ground sunlit in the afternoon; bodies of locusts on millet over long-shaded ground may be warmer than if they were on the ground. Many authors have shown (Telenga, 1930, and Lépiney, 1933, on *Schistocerca*;

Nikolsky, 1925, on *L. migratoria*; Sviridenko, 1924, on *D. maroccanus*; Kiritchenko, 1926, on *Calliptamus italicus*; and Rubtsov, 1935b, on Siberian ACRIDIDAE) that the evening ascent may occur without, or before, an evening temperature inversion and suggested that light or gravity are responsible for the ascent.

The morning ascent to the tops of millet takes place just before temperatures reverse, that is, during the first hour after sunrise. Ground in the millet is shaded at sunrise, and remains a degree or two lower than air at the millet

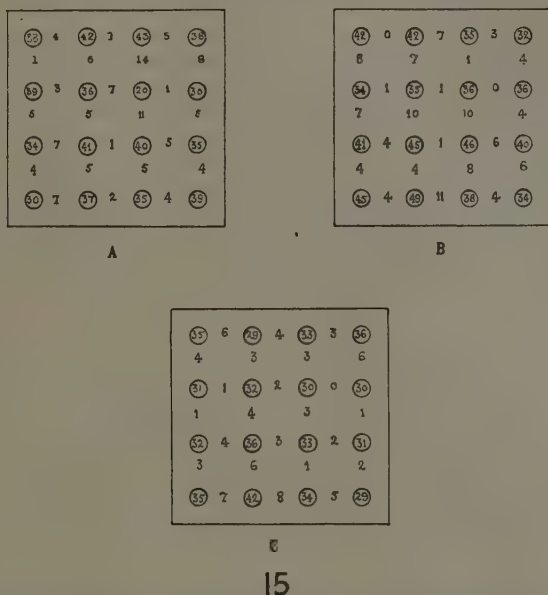


FIG. 15.—Horizontal "sun temperature" distribution on the ground on 25.ii. Thermometers arranged at regular 40-cm. intervals, irrespective of vegetation. Numbers in circles are actual readings; numbers between circles are differences between readings of adjacent thermometers.

- A: Unweeded millet (pl. 7, figs. 13 & 14, pl. 8, fig. 15); thermometers on top of ground vegetation where present, otherwise 5 mm. off bare ground. 13.47.
 B: Unweeded millet; thermometers all 5 mm. off ground whether under ground vegetation or not. 11.50.
 C: Millet without weeds (pl. 5, fig. 9, and pl. 7, fig. 11); all thermometers 5 mm. off bare ground. 14.10.

tops during the ascent. Hoppers, however, do not ascend from the ground, but from at least half-way up the stands, and between these lower levels and the tops of the stands temperature differences were less than one degree. In spite of this small gradient, bodies of the locusts are warmer up at the top of the stands in the sun than lower down in the shade (see below). Only in this sense, which excludes the possibility of a directed temperature reaction, is the morning ascent associated with temperature. Directed temperature reactions are also excluded in the evening ascent.

The morning inversion of temperature, on the other hand, was always

associated with the descent. Although only sunlit bare patches of ground were at first warmer than higher positions, yet the descent was general, and not only over bare ground. Therefore, if a causal relation exists between the morning inversion and the descent, it is not direct.

The temperature differences revealed by positions at different heights do not complete the picture of the temperature field in which locusts move and to which they react in the course of the day. To obtain a complete temperature map was impossible, but nine sets of readings of horizontal temperature differences were taken in weeded and unweeded millet on 25.ii. Three of these are shown in fig. 15.

Sixteen thermometers were arranged in 4 rows of 4 at 40 cm. intervals with no regard to vegetation pattern. Fig. 15, A and B refer to millet with weeds; C to weedless millet. In A the thermometers were at the top of ground vegetation if present and just off the ground where it was bare. In B and C all were placed just off the ground. Between readings at B and C the thermometer left in one place on bare sheltered ground fell by 3° C.

To establish true relations particularly between A or B and C many more readings are required, but fig. 15 shows the patchiness of the temperature field in unweeded millet (A and B) and it was with such differences, no less than with vertical ones, that locust behaviour was correlated. The smaller differences in C probably indicate the less patchy nature of temperature field in weedless millet.

b. Body temperatures.

A needle thermocouple was used to measure internal body temperature, in conjunction with a Unipivot Galvanometer. The junction was at the end of a hypodermic needle 1 mm. in diameter. Only one needle could be used at one time. The apparatus was fitted in a wooden box stuffed with wool and covered with aluminium foil. A test was made to see if the exposure of parts of the needle and its holder, other than the junction, to the sun affected the temperature of the tip; no effect was found.

The needle was inserted in the anus and gently worked up the hind gut until the tip was in the thorax. The hind tarsi were fastened in plasticine at the base of the needle, and the insect could thus be carried on the needle. Internal damage to the insect was probable but not apparent in behaviour. If the insect seemed abnormal on removal the records were discarded.

The thermocouple was not greatly used in the field for lack of time and difficulty of comparing body temperatures in different positions with only one needle. Several times the temperature of a locust's body was compared in the sun and the shade at the top of millet within an hour after sunrise. The body was up to 2° C. warmer in the sun than in the shade, showing that temperature may play a part in the morning and evening exposure of bodies to sun, apart from light effects.

In morning or late afternoon, body temperature was usually 2-5° C. above the reading of the plain thermometer, but near the midday ascent time it was often 10° and sometimes 12° C. higher, but sometimes 5° or even 10° C. lower than thermometer readings. These anomalies were not apparent below 32-33° C., but above this diverse readings of body temperature were obtained.

Many more temperatures were taken at camp where changes according to exposure to sun and wind could be studied more conveniently. Screens were arranged on a table and continuous records made of body temperature in

different exposures at different times of day. Three long continuous records were made with green 5th instar hoppers and one with an adult, and figs. 16-18 show some of them with parallel readings of a plain and black-bulb (not *in vacuo*) thermometer. Figs. 16-17 show body temperatures of hoppers, when a fixed arrangement of wooden screens was used giving four types of exposures.

The same difficulties of measuring air temperature arose here as in the field. A thermometer under a small wooden shade sheltered from wind responded to changes in solar radiation, presumably through re-emitted radiation from the table, etc. No other shade thermometer was used in the record in fig. 16, and air temperatures were estimated by interpolation between readings of the plain thermometer alongside the hopper when shaded from the sun and exposed to the wind. For adult body temperatures (fig. 18) parallel readings were taken in the shade and wind throughout. The free circulation of air round the impaled locust made the temperature in the shade and wind much the same as that of air alongside the locust in any exposure. In the adult record, the hinged screen arrangement shown in pl. 9, fig. 18 was used, and the locust had not to be moved; continuous records during the change of exposure were made. Galvanometer and thermometer readings were taken at intervals of one minute or less, and the points are not entered in the figures.

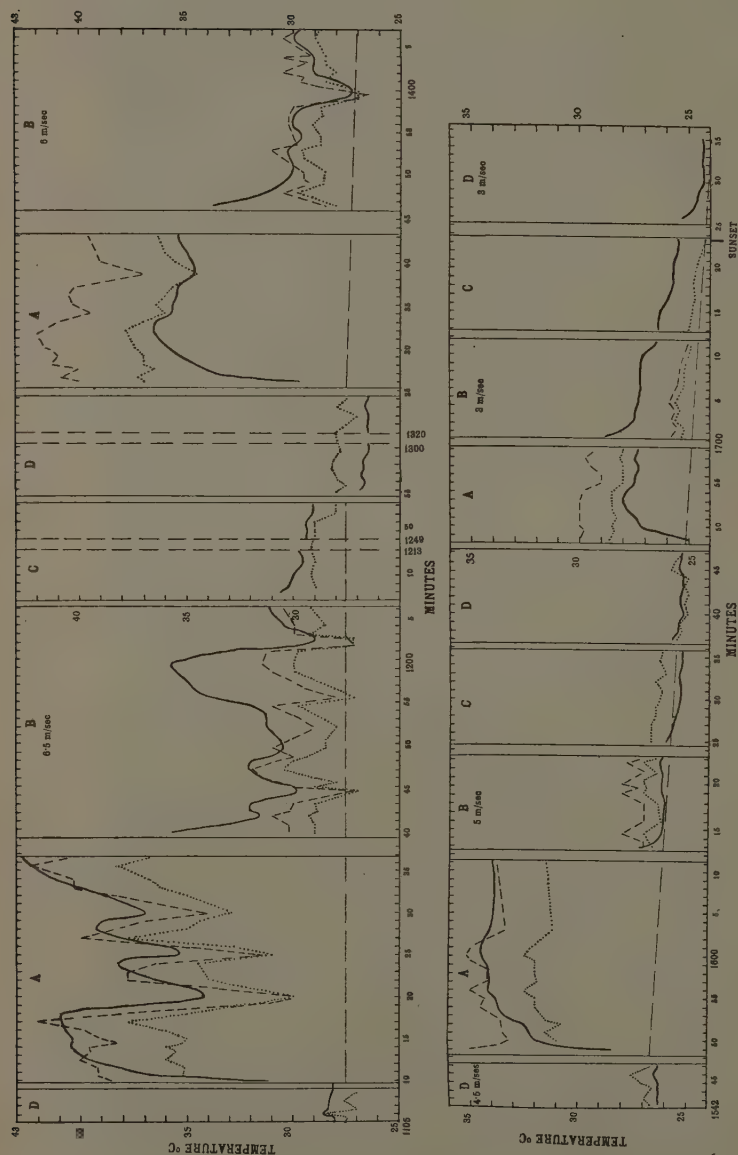
All three figures show that the body temperature is higher in the sun than in the shade within 20 minutes before sunset, and fig. 16 shows that this may be so even in wind where the locusts would be at this time (among millet heads). The possible rôle of temperature in the evening exposure of bodies to the sun is evident (see also Strelnikov, 1936a). Therefore, the lack of difference in thermometer readings in the field at this time does not indicate that there is no difference for the locusts.

The great cooling effect of the wind, which can reduce the body temperature in the sun to near the air temperature, even when radiation is strong, is also evident (fig. 16, 11.40-12.06, 13.46-14.07) and wind can also reduce body temperature in the shade. The records show that temperature changes are "damped" in the insect's body, small changes recorded by thermometers not having effect, and large ones lagging behind. This is well shown in fig. 16, 11.10-11.37, when broken clouds passed over the sun.

Fig. 17 shows the fall in body temperature below air temperature after sunset. Readings were taken under a screen where radiation away from the body would be retarded. Strelnikov (1936a) shows greater relative depression of body temperature in *Locusta* in the field.

Adult body temperature was higher in relation to the thermometers than that of the hopper under similar conditions, and exceeded that of the black bulb in the sun, above which the hopper's body temperature rose only rarely.

There is more variation in the records between body temperature (in sun and shelter) than suggested by Bodenheimer (1929), according to whom it rises quickly to over 40° C. in the sun in the morning and remains at 40-45° C. during the day. There is evidence that the insects alter their own body temperature in certain conditions without moving, *e.g.* in fig. 16 the temperature of the hopper followed the black bulb closely from 11.10 to 11.37 (34-42° C.), but when put next in the sun and shelter (13.23-13.43), the black bulb remaining at its high level, the hopper's temperature did not reach even that of the plain thermometer. When again exposed to the sun in shelter (15.50-16.10) the body temperature again rose to that of the black bulb, which had now fallen to 33-35° C. The gap between adult body temperature and that of the black bulb was reduced in a less striking way between the 10.39-



16

FIG. 16.—Changes in internal body temperature of a green 5th instar hopper under various conditions of exposure, in relation to thermometer readings, on a table in the open during 28.ii.

Continuous line, internal temperature of the thorax, thick broken line, black-bulb (17 mm. long, 3 mm. diam.) thermometer (not *in vacuo*) alongside hopper; dotted line, plain thermometer (similar-sized bulb) alongside hopper; thin broken line, approximate air temperature in shade and wind. Double vertical continuous lines indicate times when hopper was moved from one exposure to another; double vertical broken lines indicate periods omitted from the figure without change of exposure.

A: Exposed to sun and in shelter of wind screen.

B: Exposed to sun and exposed to wind.

10.54 and 12.28–12.44 sets of readings, when temperatures were also generally high. Whilst suggestive, this does not prove that regulation can occur.

All simultaneous readings of hopper body and black-bulb temperatures taken either on the table or in the field in sunny sheltered positions are therefore included in fig. 19, as well as some taken inside the wire gauze cases (see below and pl. 9, fig. 18). Only one representative reading was used from each set in fig. 16. Unfortunately few readings were taken with the black bulb above 36° C.

Despite its lighter colour, the hopper was usually warmer than the black bulb up to 32° C.; above this the points scatter widely and some appear below the line along which black-bulb temperature equals body temperature. The relation between the two appears unstable over this black-bulb range, as was noticed in the field. When black-bulb temperature exceeded 36° C. none of the nine readings shows a body temperature higher than the black bulb.

Diverse conditions under which the readings were taken do not appear to

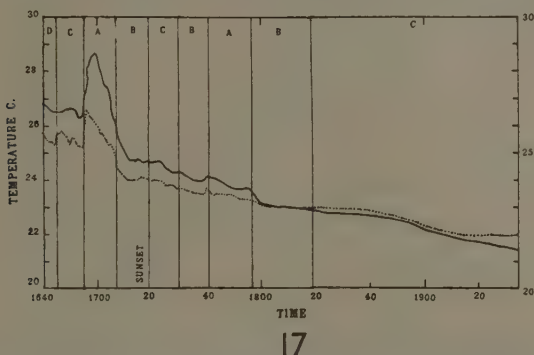
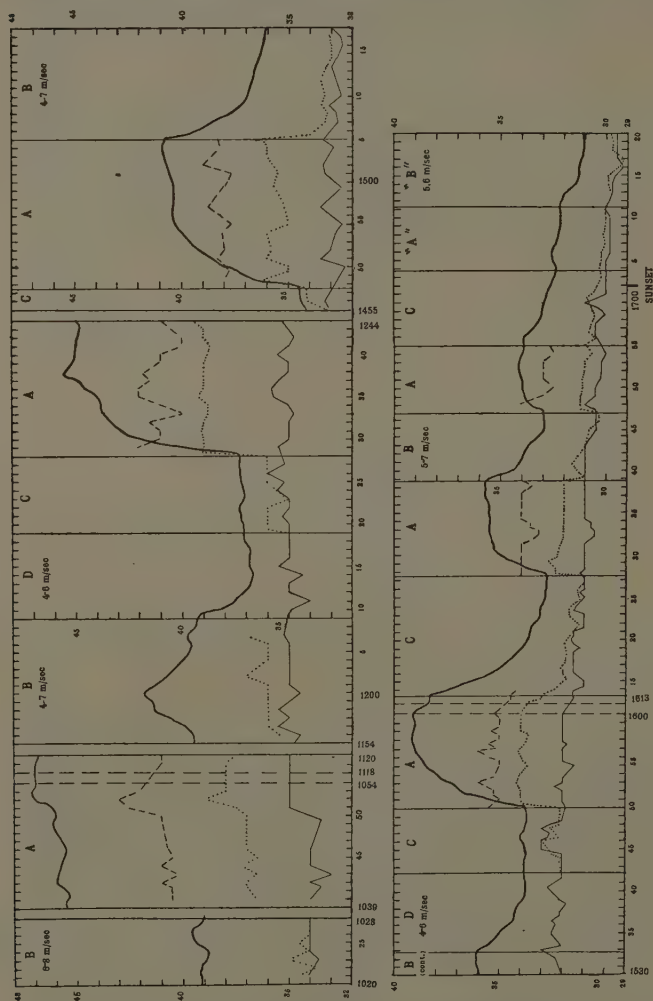


FIG. 17.—Changes in internal body temperature of a green 4th instar hopper on a table in the open, before and after sunset on 27.ii. Vertical lines indicate changes of exposure. Otherwise as fig. 16.

account for this change in relation of thermometer to body temperature, and a process of regulation seems to be at work, probably based on increased transpiration at high temperatures. It is possible that increased ventilation also helped to cool the insects, but heat so lost is probably small compared to that lost by evaporation. Buxton (1924) showed body temperature to be higher in dead than live grasshoppers and suggested evaporation during respiration as the cause. Increased evaporation at high temperatures is a well-established phenomenon in insects, and Necheles (1924), Mellanby (1932) and Koidsumi (1934) have recorded a regulation of body temperature at high external temperatures, and suggested that increased evaporation is responsible. The phenomenon, while not mentioned by locust investigators, is therefore not unexpected.

A plain uncoated thermometer is not affected by radiation as much as the hopper's body or an unenclosed black bulb, and its readings cannot be directly compared with body temperatures as in fig. 19, without reference to air temperature, often unknown. If this be ignored, the relation between plain thermometer temperature and body temperatures plotted as in fig. 19 shows the latter higher than the thermometer up to 31–32° C., and then scattered read-

ings varying from body 12° warmer, to 10° cooler, than the thermometer. These relations cannot be transferred to the field to give estimates of body temperature in terms of readings of "sun thermometers" obtained in all-day records,



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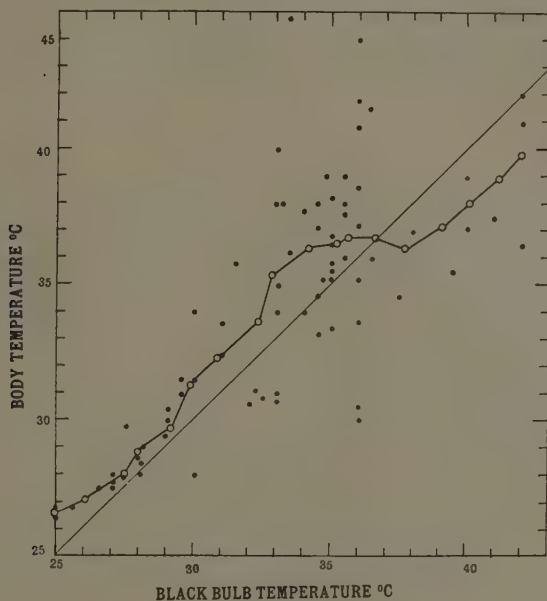
FIG. 18.—Changes in internal body temperature of a grey adult female on a table in the open, during 22.iv. Thin continuous line, readings of thermometer in shade and wind. Single continuous vertical lines indicate changes of exposure; double continuous vertical lines, changes of exposure and periods omitted from the figure; double broken vertical lines, periods omitted without change of exposure. Otherwise as fig. 16.

owing to variation in meaning of "sun thermometer" (in terms of body temperature) with varying intensities of radiation, and to the unreliability of air-temperature readings in the field.

It is possible, however, that in the morning basking period body temper-

ature, at first several degrees above the thermometer, varies greatly as temperature rises in the thirties, the net effect being that the average rise in body temperature of all basking hoppers above 36–39° C. is arrested and not resumed until basking-place temperatures rise over 40° C., when hoppers leave the basking-places.

Body temperature regulation may be effected by locusts in the field (i) by changing the body orientation in relation to heat rays (Fraenkel, 1929; 1930;



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FIG. 19.—Relation between readings of internal body temperature of green 5th instar hoppers in sun and shelter, whether on a table or in the field, to readings of black-bulb thermometers alongside the hoppers. Illustrating temperature regulation.

Body temperature equals black-bulb temperature along the thin diagonal line. Empty circles joined by the thicker line are "overlapping averages." Each point represents the average value of readings falling on or between three consecutive degrees on the black-bulb temperature scale, say 30, 31 and 32, the next point being averaged from readings on or between 31, 32 and 33.

Bodenheimer, 1929; Strelnikov, 1936a); (ii) by changing the rate of evaporation; and (iii) by moving from one situation to another.

Strelnikov (1936a) studied body temperature of *Locusta* with multiple thermocouples, enabling the simultaneous taking of readings in a number of positions. These were correlated with the various phases of the daily routine, taking account of sun, wind, body pigmentation, orientation, and other effects in an exhaustive and illuminating manner. He does not mention the "passive" type of body temperature regulation.

Highly important as body temperature undoubtedly is in behaviour, it is possible to exaggerate it. Uvarov (*in* Hussein, 1937) wrote: "... the experi-

ments have proved most conclusively that the behaviour of locusts is governed by the temperature of the environment not directly, but through their body temperature." Hussein's experiments proved that the physiological state and general activity level depend on body temperature, but unless it be assumed that heat receptors are not present on the body surface, effect of external temperature in the form of reflexes linked with surface receptors must be admitted as equally important. For instance, avoidance of bare ground at midday on hot days, is an instantaneous reaction occurring before internal body temperature is able to reach a new steady state. Effects of internal body temperature constitute only a foundation on which a whole complex of secondary effects is superimposed, when dealing with individuals in a patchy temperature field.

(ii) *Humidity.*

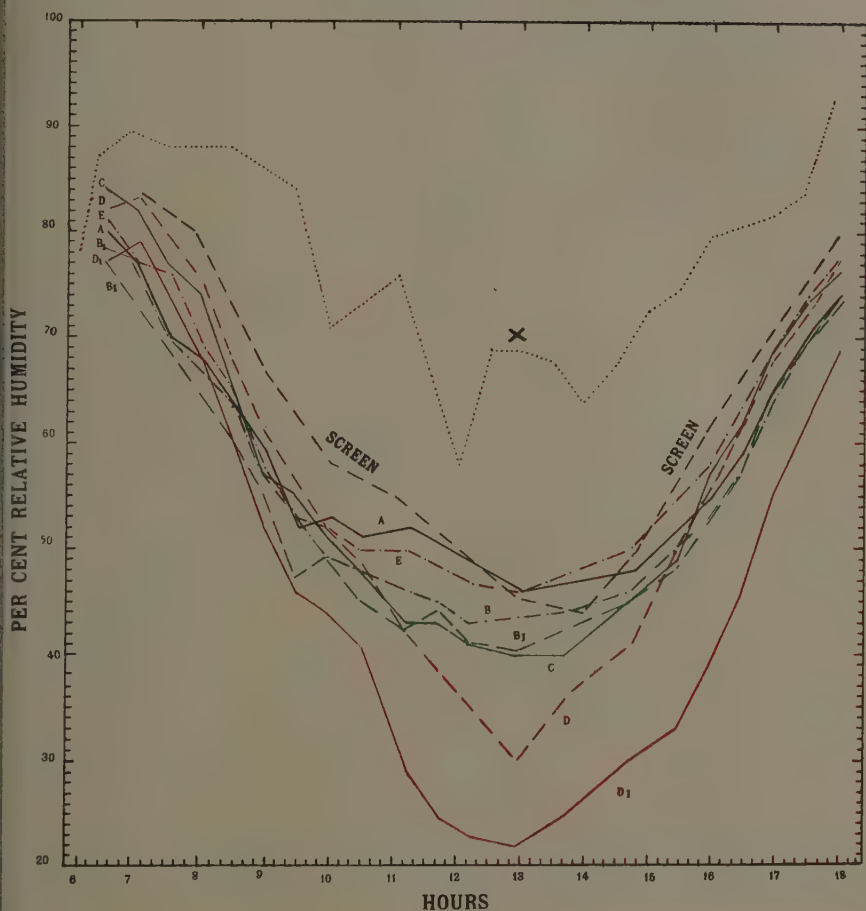
Difficulties of attempts to measure air temperature in the field were even more acute with humidity. Edney paper hygrometers (Gunn and Kennedy, 1936) were used because they could be read quickly and easily without mixing of air. The range over which each hygrometer had to work was restricted as much as possible, by use in similar positions. They were frequently checked against an Assmann Psychrometer inside the hut. When checking readings of hygrometers suspended under the wooden shades against the Assmann Psychrometer in the sun, on sheltered ground with no undergrowth, the error was found to reach 10% relative humidity.

With the true absolute humidity and air temperature known from the Assmann, the temperature of the sensitive paper inside the Edney hygrometer could be estimated from the relative humidity it showed. The maximum by which it exceeded the true air temperature was as much as 7° C., while the maximum error in the shade thermometer was only 2° C. (see above).

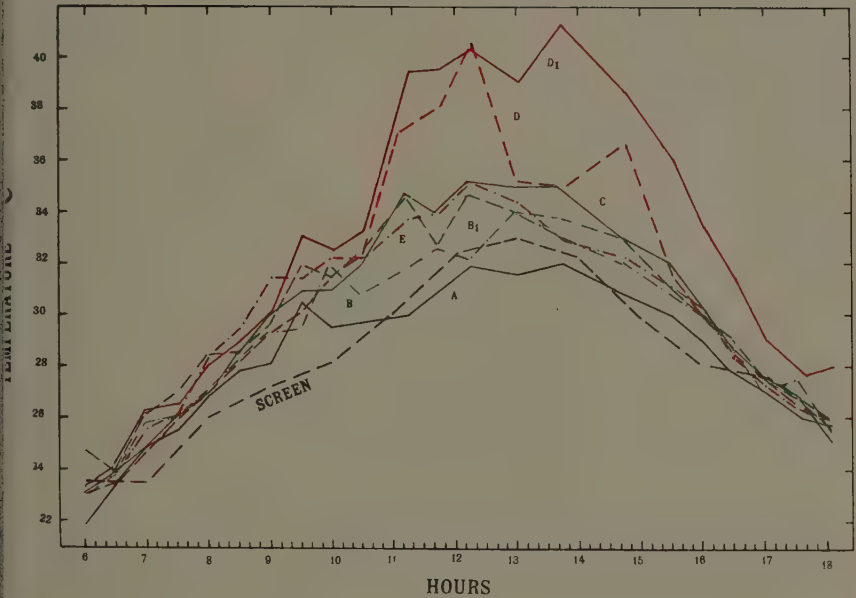
The hygrometer apparently intercepted more re-emitted radiation than the thermometer bulb, but why is not clear. The number of checks of the Edney hygrometers with the Assmann Psychrometer in the field was insufficient to calibrate the former with the latter, and the Assmann was unable to record true air temperature and relative humidity in some positions. Hygrometer readings could therefore not be corrected.

Fig. 20 shows the relative humidity readings in selected positions on 16.ii., not corrected for effects of radiation. The apparent great drop in relative humidity in the two ground positions (D and D₁) at midday and the apparent change of position D from the moistest available to being next to the driest are probably artifacts, since at midday the error due to radiation is at a maximum, and is most marked in ground positions. Fig. 21 shows the uncorrected shade temperatures in the same positions on the same day. Fig. 20 forms a basis to consider some aspects of the real humidity field in unweeded millet and its relation to locust behaviour.

The range of relative humidities, while considerable in time, is narrow in space at any one time. Even with no allowance for effects of radiation, the maximum range on 16.ii. at 12.15 was about 25% between A and D. On 16.ii. no instruments were in the interior of dense undergrowth, mainly because locusts seemed to spend little time there. On 12.ii. a thermometer and hygrometer were set at the bottom of 40-cm.-deep grass and, with this position, maximum relative humidity range (at 13.00) was 35%, from 69% to 24%, again with no allowance for overheating the hygrometers on bare ground. 12.ii. was



Readings of Edney paper hygrometers under small wooden screens (pls. 7 and 8) in the same selected positions in unweeded millet, and on the same day, as those in figs. 10 and 21. Lettering as in fig. 10. Errors due to radiation not corrected (see text).



Readings of thermometers under small wooden screens in the same positions in unweeded millet, and on the same day, as those in figs. 10 and 20. Lettering as in fig. 10. Errors due to radiation not corrected.

less sunny than 16.ii. and bare-ground positions were not so hot and apparently dry as on 16.ii. Humidity readings under deep grass on 12.ii. are shown on fig. 20, and it may be seen that if humidity in grass on 16.ii. had remained as high as on the 12th the apparent range would still not exceed 45%. This ignores the fact that air temperature would have been higher and hence relative humidity lower in dense grass on 16.ii. It must be remembered that when apparent relative humidity range was at a maximum, the hygrometer in the driest position read as much as 10% too low; that at other times of the day even the uncorrected range is much narrower; and that locusts seldom entered dense undergrowth where the highest humidities occur, so that the true range encountered during most of the day is between 10% and 20%. The narrowness of this range raises doubt as to reactions to relative humidity being important in daily behaviour regime, unless *Schistocerca* is more sensitive than *Locusta* is in the laboratory (Kennedy, 1937).

This doubt is increased by closer consideration of behaviour in relation to available humidities. In the morning and afternoon basking periods relative humidity in basking-places in dense millet and quite surrounded by grass clumps (D) was higher than A and B on the stands. The difference, though small, was greater than shown in fig. 20, since the depression of apparent relative humidity was greater on the ground than up on the millet. There is a gentle vertical humidity gradient over such ground. The slightly higher shade temperature at D is not enough to compensate for the higher absolute humidity, by reducing relative humidity to, or below, that of A and B. This might suggest a "preference" by hoppers for moister air, but if so the preference was not strong at all parts of the humidity range, for in dense grass the air was moister but no hoppers were there. The alternative hypothesis of preference for an intermediate humidity region ("optimum") is equally untenable, for relative humidity changes continually in the "preferred" position (D), and values found there at one time were found elsewhere (grass, or up on millet stands) at other times on the same day. This is made clear in fig. 20, even after full allowance for errors due to radiation.

In parts of the field where millet stands grew less thickly, more wind penetrated, undergrowth was thinner and bare ground extensive (pl. 8, fig. 16), absolute humidity was not high enough on the ground to compensate for the higher temperature, and relative humidity was lower than in D (pl. 8, fig. 15). For example, at 09.00 hours the "sun temperature," air temperature and relative humidity at D were 30°, 29.3°, and 61% respectively, while at D₁ they were 31°, 30°, and 52%. An air temperature of 29.3° and relative humidity of 61% indicates an absolute humidity of 17.7 gm./m.³, giving at 30° a relative humidity of 60%. The 8% difference between 52% at D₁ and 60% at D could not be explained by differences in radiation errors; yet hoppers were basking at both D and D₁ at the same time.

In the absence of undergrowth in the millet the decrement in the vertical humidity gradient appears in fig. 20 to pass from the top to the bottom (B₁ and D₁). It is more difficult here to allow for radiation error, and the gradient may actually pass in the opposite direction, i.e. as with dense undergrowth, but were this so the gradient is much less steep than in millet with dense undergrowth, and yet hoppers basked on the ground most of the day.

Thus, despite errors in humidity readings, there seems no evidence of reactions to relative humidity playing an important part in the diurnal regime. For locusts to react to the humidity field they encounter, great sensitivity to humidity would have to be postulated, and even so no evidence of an absolute

moist or absolute dry preferendum, or one for an intermediate region of the humidity range was found.

In literature on diurnal behaviour it is sometimes mentioned that humidity is important but, owing to the difficulty of separating humidity and temperature, proof is hard to obtain. Maxwell-Darling (1936) took readings with a whirling hygrometer on the Sudanese coast and concluded that the differences were of little account, with which my observations agree, although the positions in which he took readings appear not to reveal the moderate differences which exist. Zolotarevsky put most emphasis on humidity (1933). The optimum for adults (*L. migratoria capito*) is said to be about 60%, for hoppers 70%, and movements, large in adults and small in hoppers, are said to be caused by deviations from the optimum. This has been discussed on p. 481. Laboratory experiments (Kennedy, 1937) on *L. m. migratorioides* showed no evidence of an "optimum" humidity, and Zolotarevsky's observations may be explained by other factors, particularly temperature in the case of hoppers. Similarly the effect of humidity on the movements of Siberian ACRIDIDAE, suggested by Vinokurov and Rubtsov (1930) and Rubtsov (1935b) cannot be separated from temperature effects. In this case laboratory experiments also indicated a "preference" for high humidity in *Chorthippus albomarginatus* consistent with the field observations. Experiments on carefully quietened *L. m. migratorioides* near-*gregaria transiens* (Kennedy, 1937) showed a weak avoiding reaction away from the higher of any two humidities in any part of the humidity range, and a weak positive hygrokinesis. Key (1936) found slight negative hygrokinesis in different conditions and Edney (1937) obtained little or no evidence either way.

There is then little conclusive evidence that humidity is generally important, and its rôle remains in doubt.

Note.—Michelmore is of opinion (1934) that "Unless insects are equipped with special sense organs for the perception of humidity, the only way in which locusts can be affected by the dampness of the air is by its effects on the loss of moisture from the body. Humidity should therefore be measured as saturation deficiency or evaporating power." Nevertheless in the above discussion relative humidity and not saturation deficiency is referred to.

In relation to water loss and general vital processes in insects, it is usually agreed that saturation deficiency is a better measure than relative humidity (Buxton, 1932; Ramsay, 1935). This seems no adequate reason to assume that it is a better measure in relation to behaviour. Incidentally, Hamilton (1936) found relative humidity a better measure than saturation deficiency in relation to development in *L. m. migratorioides*, *S. gregaria*, and *Nomadacris septemfasciata*.

In laboratory experiments on *Locusta* hoppers I found (1937) a dry preference in a chamber with 60% relative humidity difference at 30° C. and 5 metre-candles. With increased illumination they became more active and their humidity reaction less apparent. Lower temperature decreased activity so that humidity reaction became again weaker. With illumination increased and temperature lowered to 20° C., thus maintaining an activity level similar to that at 30° C. and 5 metre-candles, reaction was if anything enhanced. Yet at 30° C. a 60% humidity range from 20% to 80% represents a saturation deficiency range of 18 gm./m.³, whereas at 20° C. the same relative humidity range represents a saturation deficiency range of 10.2 gm./m.³. In other experiments decreasing the relative humidity range caused a weakening of the reaction, but decreasing the saturation deficiency range, as above, did not.

This has not been considered by other authors, but Thomson (1938) found a strong avoiding reaction against higher relative humidities in blood-fed *Culex fatigans*, but it was only evident if the humidity gradient in the Alternative Chamber included 90% relative humidity; moreover, this was the critical point whether the temperature was 20, 25, or 30° C., so that expressing the results in terms of saturation deficiency would conceal the consistency.

Thus it seems that relative humidity is more relevant to behaviour than saturation deficiency, and that insects are "equipped with special sense organs for the perception of humidity." Fuller confirmation is required, but until disproved this working hypothesis may be suggested:

Although metabolic processes may often be better related to saturation deficiency than relative humidity, the humidity receptors carried by insects are more in the nature of hygrometers than evaporimeters.

(iii) *Wind.*

Instruments available at Hamashiameb to measure wind speed are mentioned in the Appendix. The airmeter, although cumbersome, was the more accurate and sensitive, the "Wind Speed Indicator" was less so, but handier, and could be used in small places and close to the ground. No wind speed instrument, giving, that is, the speed of a current of air assumed uniform and uni-directional, is suitable for measuring wind in vegetation where currents are extremely complex. For locusts the most relevant aspects of "wind" are mechanical agitation by air movement in all directions, and the rate of replacing air at the body surface (affecting evaporation and cooling) in different situations. These could not be measured, and wind data are few and inaccurate.

Figures of relative wind speeds on 16.ii. recorded by the airmeter are given in fig. 10. All-day records in the selected positions where thermometers were also being read, and where behaviour was followed, were taken on only one day, 27.iii. These serve to illustrate relative wind speeds in different positions in weedless millet near the mouth of Khor Toqwan (pl. 6, fig. 11). The indicator used already showed zero in places on the ground in the shelter of millet stand bases in the absence of weeds, and was incapable of showing, as did the smoke of a cigarette, that the ground in weedless millet was draughtier than that among undergrowth in millet. Wind higher up the stands did not differ consistently in weeded and unweeded millet.

The records given in fig. 22 are therefore probably as typical of general relations in unweeded as in clean millet. No indigenous hoppers were present on 27.iii., and notes on hopper behaviour refer to extreme *dissocians* green-coloured, 5th instar, hoppers, which very closely paralleled that of indigenous hoppers.

Wind on the ground in a sheltered position (D_1) remains virtually unaffected by wind changes outside the millet (E and F) and at less than 0.5 m./sec. throughout the day. Position C, 15 cm. off the ground, but also in shelter, is slightly windier than the ground position, and B_1 , 60 cm. off the ground, is again slightly windier, but all receive only a fraction of the wind at A among millet heads, where the windiness, without reaching, approaches that of completely exposed positions (E and F).

While higher positions are windier than lower ones in the day, the mechanical stimulating or cooling effect at higher levels does not prevent most hoppers being there in early morning, at midday and in the evening. Moreover, when hoppers are basking on the ground, the shade is as calm as or calmer than the sun, so that wind does not explain horizontal distribution of the hoppers on the

ground. The morning increase of wind at higher levels is associated with the morning descent and the evening decrease with at least the latter part of the evening ascent period (Strelnikov, 1936a). The evening ascent, however, begins before the wind has dropped to a strength comparable with that before the morning descent began. This was often observed, and does not simply imply that the hoppers were not yet at the highest levels; for most hoppers this was the case, but some climbed to the windy levels well before the wind had dropped especially when the ground below became shaded. The time of the morning descent and evening ascent was observed to vary from place to place on the same day according to when the ground was exposed to, and shaded from, the sun, so that the association with rise and fall of wind was only

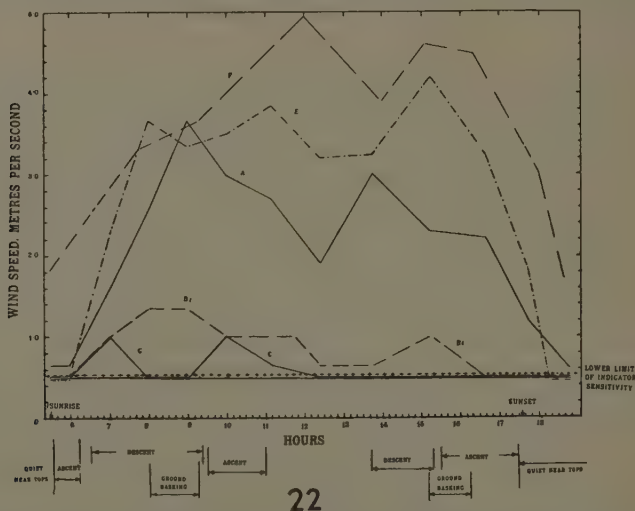


FIG. 22.—Wind speeds as recorded by the "Wind Speed Indicator" in selected positions in millet without weeds during 27.iii., and outline of behaviour of the majority of green solitarily-living *dissocians* hoppers in the vicinity.

F: 1.5 m. off ground outside millet over bare exposed dune.

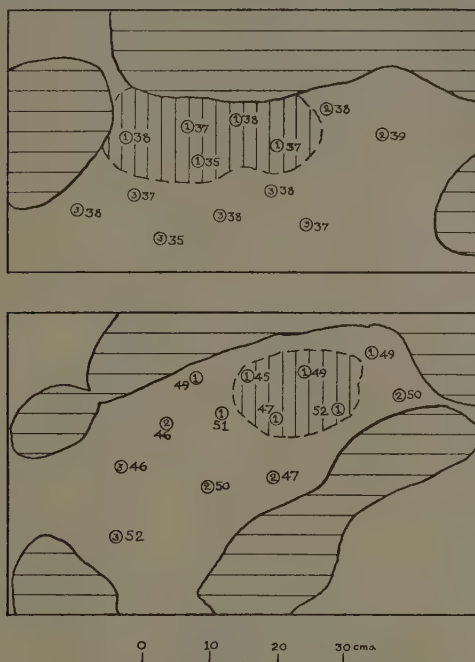
For remaining lettering see fig. 35.

approximate. The midday ascent and descent were not related to changes in wind strength.

Therefore, as regards the mechanical effect of wind, evidence of association with behaviour was obtained only in the morning and evening, but the cooling effect, so important for locusts spending so much time in the sun, must also be considered, and the morning descent and group formation is probably connected with the combined effect of temperature and wind at higher levels. The midday break up of groups and ascent help hoppers to reach positions that are cooler not only because of decreased reflected radiation and air temperature, but also of increased air movement. The evening ascent carries them to windier places but radiation and wind are now weak and the cooling effect correspondingly less. Wind appears to play little part in the morning ascent.

Some evidence was obtained that hoppers could respond to mechanical or

thermal effects of slight air movements not registered by the instruments. Fig. 23 shows sun temperature and wind "maps" of two basking-places in dense irregular vegetation at the extreme north of the Khor Toqwan cultivation. Midday readings were taken on 25.iii. with no hoppers basking in either place, but the relation of temperature and wind distributions are relevant. If only the temperature readings are considered there is no apparent reason why groups



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FIG. 23.—“Sun temperature” and air movement readings on the bare ground of two “basking-places” in unweeded millet at midday on 25.iii. Illustrating the correlation between basking hopper distribution and small air currents.

Figures in circles refer to the behaviour of the smoke trail from a cigarette at the positions indicated: 1, rising straight upwards; 2, eddying; 3, streaming along the ground. Figures outside circles indicate the “sun temperature” reading at the same positions. Vegetation shaded with horizontal lines; area occupied by the members of basking groups shaded with vertical lines.

should be restricted to the positions occupied prior to midday. However, when the smoke-trails of a cigarette are considered at the various points, the confinement of all basking individuals in a comparatively small area seems explicable by air movement, rather than, as appeared at first sight, by gregariousness. Similar results were obtained from three other basking-places.

The basking-places studied were all in the above-mentioned strip of cultivation which was penetrated by wind to a greater extent than places in the

middle of the thick unweeded millet. On the latter the confinement of basking individuals to one portion of the small area of bare ground equally well exposed to sun was not noticed. Basking on larger bare patches in millet (pl. 8, fig. 16) was always confined to a few situations close to the margin of the undergrowth. Here again an impression of gregarious behaviour was obtained, but it is more likely that local conditions of air movement were responsible. Even here, temperature effects predominate over wind effects since equally calm air was always available in the shade where hoppers do not sit, as well as on the basking-places proper.

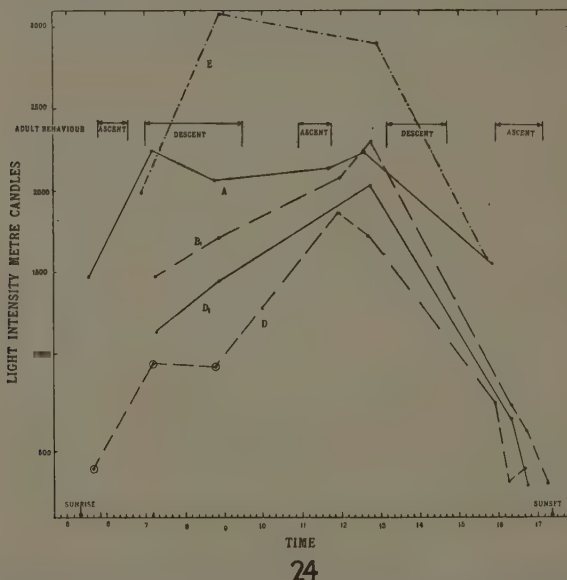


FIG. 24.—Average illumination intensities as recorded by an Exposure Meter at selected positions in millet without weeds, at times when the sun was out or shining through thin white cloud, during 8.iv., and vertical movements of solitarily-living *dissocians* adults in the vicinity. All readings were taken when the positions concerned were exposed to the sun, except the three points in circles at D.

Each point represents the average of six readings: upwards and downwards, and N, E, S and W, unless the direct rays of the sun entered the instrument, in which case the remaining 5 readings are averaged. D: on ground among dense millet (pl. 6, fig. 11); other lettering as in fig. 35.

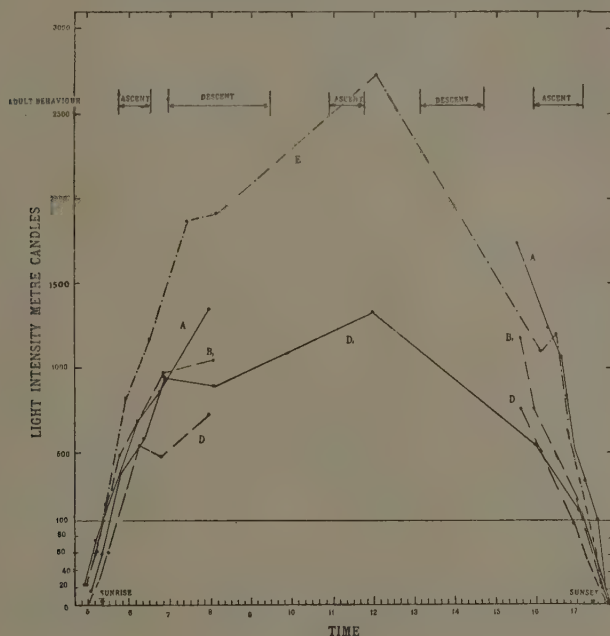
(iv) *Light*.

The Weston Exposure Meter was used twice, on 8.iv., and the morning of 12.iv., in relation to diurnal behaviour and both times in clean millet with only *dissocians* adults present.

The rays impinging on the photo-sensitive surface being restricted to a narrow cone, 6 readings were taken in each position. They were taken without regard to neighbouring vegetation with the instrument directed north, south, and west and vertically upwards and downwards, the observer interfering as little as possible with natural incidence of light. In ground positions the instrument

was raised for vertical readings 8–15 cm. off the ground to prevent its shadow entering its field and to enable the observer to see the scale on the back of it. When not in use it was kept in shade with its face covered.

The effect of cloud and of variations in cloud density on light intensity are more profound than on other micro-climatic factors discussed, and great differences were found at the same place within a few seconds. Readings on 8.iv. are therefore divided in two sets; one incorporated in fig. 24 includes all readings taken when the sun was out or shining through very thin cloud; the



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FIG. 25.—Average illumination intensities at the same positions and on the same day as those in fig. 24, at times when the sun was obscured by cloud or below the horizon. Otherwise as fig. 24.

other, in fig. 25, includes all readings with the sun obscured. This is necessary to make the figures comparable, but much reduces the number of readings in each graph. None was in any case taken between 08.40 and 11.30, or between 12.50 and 15.40. The joining of points across these periods does not represent the real conditions. Although the readings were taken in weedless millet, D was not dissimilar, as concerns light conditions, from a basking-place in unweeded millet, for it was surrounded with vegetation (like ground in pl. 6, fig. 11). Position A, by the millet heads, being also in very dense stands, was similar to A on 16.ii. in unweeded millet. B₁ and D₁, however, were in the lee of a stand to the north of a clearing with bare sand, and doubtless received more reflected light from below, and from east and south (not from west where

the ground sloped and only millet was in the line of view of the photometer), than was the case at D, D₁, B, and B₁ on 16.ii.

The 6 readings taken at each position were averaged to give the figures plotted on the graphs. Full set of readings were not taken inside vegetation, such as inside bases of the millet stands.

Figs. 24 and 25 are both compatible with the expectation that light reflected from the sky is usually more intense than from bare sand, and that from bare

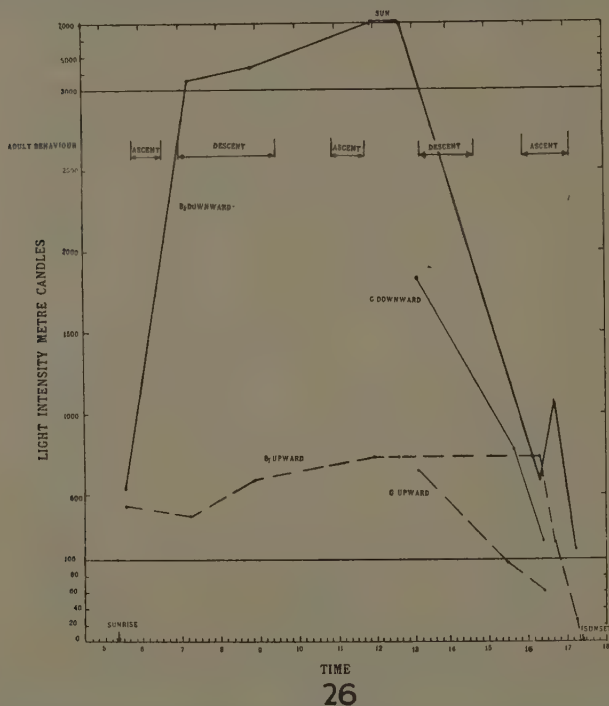


FIG. 26.—Vertical illumination intensities 90 cm. off ground on the same day as figs. 24 and 25, at times when the sun was out or shining through thin cloud. Light scale expanded at bottom, contracted at top.

B₁: Outside a millet stand on the lee side of a clearing among millet.

G: In the interior of a single thick millet stand.

sand more than from vegetation; and that the relations between the average intensities in the various positions depend on the different proportions of incident light received from these three sources. It seems that relative light intensities in any zone can be estimated on this basis.

Basking group formation cannot be correlated with light intensity. Were locusts strongly negatively phototactic, or positively photokinetic, they would be found in shade or in vegetation, not in the sun. If, however, they were strongly positively phototactic or negatively photokinetic, they would be higher up from the ground where more reflected light from the sky would reach

them. Nor could the midday break-up of groups be correlated with light intensity, for they became scattered both inside and outside the millet stands, where light intensity may be either higher or lower than on the abandoned basking-places.

Since ascents and descents are made on more or less vertical stems one may consider relative vertical light intensities, separated from horizontally incident light. Figs. 26 and 27 show readings of vertical light intensity half-way up a

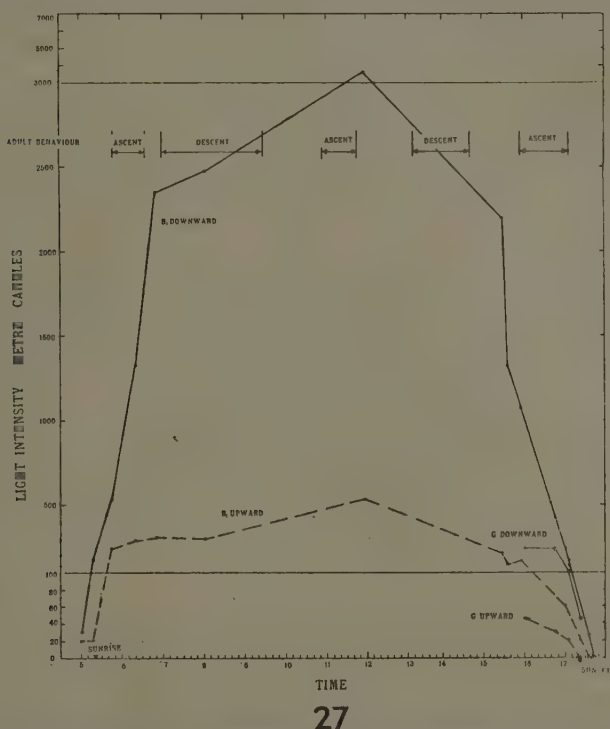


FIG. 27.—Vertical illumination intensities at the same positions, on the same day as in fig. 26, at times when the sun was obscured by clouds or below the horizon. Light scale expanded and contracted as in fig. 26. Lettering as in fig. 26.

stand. Most apply to a position outside a millet stand (B) but some inside the middle of a stand are included. The relation between the upward and downward light at the position outside millet at 16.20 in fig. 26 represents an occasional exception to the statement that light reflected from the sky is always more than from the ground. This was due to grey clouds overhead while the sun had just emerged from the edge of a cloud-bank and shone from low in the west on light-coloured ground.

The morning ascent occurred before normal daytime intensity of downward-directed light (over 3000 metre-candles with the sun out). The time was noticed to be closely connected with sunrise in this way and was roughly correlated with the relatively low light intensity. It is known (pp. 492-494) that,

other things being equal, most Acridids are positively phototactic, at least at low light intensities. At the time of the morning ascent other conditions are more nearly equal than at other times and it is possible that positive phototaxis assists the morning ascent.

Placing of the body exposed to the sun was concurrent with the morning ascent. This was also noticed in locusts inside the hut, on millet at night, and on millet in a room in relation to "cold" light (pp. 450 and 493). Thus here, as with similar exposure to the setting sun's rays after the evening ascent, light as well as the small thermal effect of radiation may play a part.

The morning descent, midday ascent and descent and evening ascent were not, however, associated with particular hours. The morning descent and evening ascent occurred at different times in different places on the same day according to density of millet, that is, the degree of wind penetration or the time at which ground became, or ceased to be, exposed to the sun. The evening ascent might be well advanced in dense millet, with shaded ground, before it started in less dense millet. Downwardly-directed light would be the same whatever the density, but not upwardly-directed light and, in dense millet, more like that in the stand in figs. 26 and 27. Thus the evening ascent might be associated with degree of contrast between upward and downward light, as well as the general low intensity (positive phototaxis). The morning descent occurred, however, with light intensity high and the contrast between upward and downward light less than before the ascent began. The midday ascent and descent occurred with light conditions very similar, and contradict one another in their relations to these conditions.

The start of morning activity was closely associated with sunrise although temperatures varied considerably. Thus the onset of activity was associated with a relatively low light intensity and the beginning of a rapid increase in intensity. Its end was similarly associated with low intensity and completion of a rapid change in intensity just after sunset. That "Beginning of activity," "morning ascent" and "exposure to sun" may occur as light responses only, with no appreciable temperature change or difference is mentioned above (p. 451).

(v) *Conclusions.*

1. The beginning and end of activity was not associated with a particular temperature but with the beginning and ending of marked temperature changes. The morning descent occurred as temperatures rose and the vertical temperature gradient steepened. Basking and group formation occurred where temperatures were highest. The break-up of groups and midday ascent occurred when "sun temperature" on basking-places exceeded 40°C ., and midday descent and re-formation of groups took place when temperature there again fell to this level. The evening ascent was associated with shading of basking-places and consequent decreased steepness of the vertical temperature gradient but not always with the evening inversion of temperature.

2. No consistent association of behaviour and relative humidity could be established.

3. The mechanical aspect of wind as a stimulus is inseparable from the simultaneous cooling effect. The morning ascent usually occurred before the wind rose. The morning descent was associated with rise of the wind; the evening ascent with its dropping, but not always. Basking-places in dense vegetation were not associated with wind strength but in cultivation, where wind penetrated to some extent, basking appeared restricted somewhat by small wind currents.

4. The beginning and end of activity were associated with dimmer light and rapid change of intensity at sunrise and sunset. It began at, or just after, sunrise but ceased at, or after, sunset, light conditions being not quite identical, and temperature probably contributed to the effect. The morning ascent was associated with relatively low light intensity just after sunrise and the higher intensity of downward-directed light. Exposure of bodies to the sun during morning and evening ascents may have been connected with light as well as temperature. Choice of basking-place cannot be explained by light reaction, and the morning descent, midday ascent and descent, and evening ascent also showed no obvious connection with light.

3. *Camp Experiments.*

Some experiments on light, gravity and temperature reactions were made in cages in camp. Facilities were poor, complete control of extraneous factors impossible and results require laboratory confirmation.

(i) *Light.*

In these experiments extreme *dissocians* known to be living the life of solitaires in the field were used.

Hoppers and adults were put in cylindrical cages lying horizontally (2.5-mm. mesh wire gauze), 15 cm. diameter and 40 cm. long. The cages were marked in 4 equal parts. Preference was shown for sitting on one or other of the vertical ends, and in taking readings the number of individuals on each end was counted separately, as were those on the side walls in each of the quarter lengths. Thermometers at intervals indicated that no temperature differences existed.

The activity level varied greatly, and in experiments involving alternations in the direction of application of a stimulus or the stirring of animals, high and low activities mask any latent reaction, which can only appear with activity at a certain moderate level.

Table XXIV shows results of experiments on hoppers, where laterally impinging light was equal at both ends, but more entered from one end. In 1 to 5 cages were reversed in relation to source of light after each count, with a minimum of disturbance. In 6 to 8 the hoppers were stirred alternately to each end by tipping and shaking the cage, after each count, and the cage reversed in relation to light half-way through the experiment. In 3 the cage was in the open facing east and west; a slight north-north-east wind appeared not to affect the hoppers. In 5 the source of light was an electric torch and the intensity of illumination was below the level of sensitivity of the Exposure Meter. In 1, 2, 4, and 6 cages were placed in a bell tent lined with dark blue material, one end facing the open door. In 7 and 8 cages lay in an open space. In 8 a sloping white cotton screen shielded the cage from the sun, leaving it open to the sky to the north. In 7 a screen, six layers thick, was arranged over and on the two sides of the cage. In contrast to conditions in cages in the tents, most light in 7 and 8 came not from one end, but from the sides, although lateral light was still equal at both ends. Light from the ends was made unequal by a black disc at one end.

Counting hoppers at 6 positions along the cages enables the results to be given not only in numbers of hoppers either side the middle line, but also of effective displacements towards one or other end. Using distribution at the previous count as a basis in experiments with no stirring, or immediately after the previous stirring in others, the effective displacement at the time of the

next count was estimated in units of one hopper shifting from one division to the next. This gives a truer picture of reaction of the hoppers to light.

In 6 of the 8 experiments in Table XXIV, clear reaction towards light was shown. Experiment 4 is anomalous and not readily explained. In experiment 8 hoppers were very active under the effect of high illumination and repeated disturbance, and any light reactions were suppressed.

Table XXV shows the results of a set of experiments with similar cages placed in tight-fitting open-topped boxes. Half of each box was lined with white paper and the other half with black. Possible reaction to smell of materials was uncontrolled. In 1 and 2 the box with the cages was put in a

TABLE XXIV.

Conditions and results of experiments on light reactions of hoppers, with lateral illumination the same in both halves of the cage.

"x" denotes illumination intensity below 20-30 metre-candles. † readings taken from middle of cage.

Expt.	Date	Time	Air temps., ° C.	Approx. illumination (metre-candles)			No. of counts	Interval between counts (mins.)	No. of hoppers used	Position readings		Displacements	
				From light end	From dark end	Lateral				Light half	Dark half	Towards light	Towards dark
1	1.iv.	Midday	32	900	50	60	5	10	20	68	58	32	0
2	1.iv.	Afternoon	32-29	600	40	50	12	10	20	177	91	331	0
3	1.iv.	Sunset	23-26	550-50	300-x	x-x	6	5	18	84	30	169	0
4	4.iv.	Afternoon	36-30	700	30	45	6	20	10	30	31	22	58
5	4.iv.	Night	28	x	x	x	8	30	20	87	61	73	34
6	5.iv.	Morning	27-28	800	45	55	5	45	17	61	24	139	0
7	14.iv.	Midday	34-33	2000	100 †	840	12	15	10	79	40	162	73
8	14.iv.	Midday	34-33	2000	400 †	1200-3000	12	15	10	63	58	178	168

TABLE XXV.

Conditions and results of experiments on light reactions of hoppers, with lateral illumination different in the two halves of the cage.

Expt.	Date	Time	Air temps., ° C.	Approx. illumination (metre-candles)				No. of counts	Interval between counts (min.)	No. of hoppers used	Readings		Displacements	
				From light end	Lateral in light half	From dark end	Lateral in dark half				Light	Dark	Towards light	Towards dark
1	5.iv.	Afternoon	30-32	—	—	—	—	16	15	10	69	75	125	126
2	6.iv.	Morning	33-35	—	—	—	—	12	15	8	43	61	33	53
3	7.iv.	Midday	34-33	700	430	400	100-300	12	15	7	43	40	51	55
4	6.iv.	Afternoon	30-32	—	—	—	—	10	15	10	34	108	98	196
5	6.iv.	Morning	32-35	—	—	—	—	12	15	8	28	67	14	81
6	7.iv.	Midday	34-33	1000	600	650	200-400	12	15	7	35	50	25	65

small, closed yellow-lined tent, where light intensity was below the limit of the Exposure Meter. In 3 the thick white screen from experiment 7 in Table XXIV was used, and in 4, 5, and 6 the thinner screen of 8 in Table XXIV.

Hoppers in dimmer light, experiments 1, 2 and 3, were inactive, which may account for negative results. In brighter light, experiments 4, 5 and 6, decided preference was shown for the darker half of the cage.

Only three experiments were made on adults, in the same manner and conditions as 1, 2 and 3, in Table XXIV. In the first, readings in the half of the cage to the light were 70 and in the other 30, total effective displace-

ments being 61 to the light and none away. In the second, reaction was the same, readings being 159 and 61, and displacements 409 to the light and none away. With the adult cage in the open at sunset, alongside hopper cage experiment 3 in Table XXIV, adults moved first to the illuminated west end, but then crowded along the north side and especially in the north-east corner facing the gentle oncoming wind.

In experiments on hoppers giving positive results, reactions towards light were found at low intensities and in more or less unidirectional light, but a preference for the darker half when light was generally more intense and not unidirectional. There are three possible explanations apart from smell:—a reversal of the phototactic response at high intensity; the arrangement of a darker and lighter half of the cages allowing positive photokinesis to override positive phototaxis; or positive photokinesis acting when phototactic response had disappeared with increased illumination. Results of experiment 7 in Table XXIV make a reversal of phototaxis at moderately high intensity unlikely, but in full sunlight hoppers did tend to move from the source of light. On the other hand, differences in activity levels in different light intensities used, as well as the beginning and end of activity in the field appearing associated with particular light intensity rather than temperature, suggests that locusts are positively photokinetic. Experimental evidence of this is given on p. 451.

Similar field evidence of the importance of photokinesis in the beginning and end of activity is given by Zolotarevsky (1929) on *L. migratoria capito* and Zimin (1934) on *Calliptamus turanicus* but, since temperature change cannot be excluded, more reliance may be placed on laboratory evidence, which is good (Grassé, 1922; 1923; Everly, 1929; Key, 1936; Edney, 1937).

Most observations of phototactic response have been made at low light intensities available in laboratories and where observed the response was always positive (Fraenkel, 1929; Karandikar, 1933; Hussein, 1937; Grassé, 1922; 1923; Sviridenko, 1924; Rubtsov, 1935a). The best documented description is Grassé's in *Anacridium aegyptium* (L.), where it appears that light reaction is "telotactic," for unilaterally blinded insects responded as well as normal ones (see also Rabaud, 1921). Grassé described cases of locusts, having moved to the end of a cage through which light entered, turning their body axis perpendicular to the light as already mentioned for *Schistocerca* (p. 490). Mr. R. J. Whitney obtained evidence of broadside orientation by *Locusta* in cold light (unpublished). Reconsideration of Fraenkel's experiments (1930) on orientation of *Schistocerca* to radiant heat seems, therefore, necessary. Blinding experiments convinced him that it was a thermal response to stimuli of the whole body surface. While this still holds, it appears now that such orientation is also possible in "cold" light.

Grassé used directed light, from direct rays of the sun to artificial light, and found most rapid reaction to the former. The light impinging laterally on his cages was apparently always at roughly the same low level. This is important in relation to behaviour in the field where laterally incident light varies with the intensity of light from the brightest source. *D. maroccanus* hoppers on dull days collected on a white sheet but avoided it on sunny days (Sviridenko, 1924), but, as phototaxis and photokinesis were not separated, this cannot be taken as showing reversal from positive to negative phototaxis.

There is no evidence that phototactic responses become negative in my experiments nor in those of others, although in field observations (p. 431) there was some evidence of it. There is, however, good evidence that phototaxis

disappears when activity reaches a certain level. Fraenkel (1931), Grassé (1922) and Hussein (1937) describe a positive phototactic response evident at 20–25° C., disappearing at higher temperatures. In experiment 7 Table XXIV the response was present even at 33° C., but in 8, under brighter illumination, hoppers were too active to show consistent light response. Hussein (*loc. cit.*) found no sign of phototaxis at low activity levels associated with low temperature, and none of either phototaxis or photokinesis appeared in experiments 1, 2 and 3, in Table XXV, when low activity was associated with dim light.

It may, therefore, be tentatively concluded that phototaxis is positive at moderate or low light intensities in moderately active hoppers, but in more active ones in cages the reaction disappears. The question of reversal at high illumination intensities remains open. Positive photokinesis operates without apparent reversal.

(ii) *Gravity.*

In the few experiments on reactions to gravity diverse methods were used. Some results are given in Table XXVI. Indigenous 5th instar hoppers were used in 1, 2 and 3, extreme *dissocians* in 4. Cylindrical cages 1.1 m. by 15 cm. were used in 1, 2 and 3, in the open on the lee side of a large windscreen out of sight of camp. Vertical illumination was unequal. In 1 and 2 hoppers were not stirred nor disturbed except as a result of periodic inspections. In 3 and 4 the cage was inverted after each reading, bringing all hoppers to the bottom. In 1, 2 and 3, distribution was noted in 6 equal parts of the cages, and on the roof and floor. A hopper touching roof or floor was counted as on the roof or floor.

Temperature was recorded by ordinary thermometer inside the cage. In 2 and 3 the cages rested on the ground, in 1 and 4 it was 1.5 cm. above it. In the Table XXVI the first temperature reading of the day is given, that at

TABLE XXVI.

Conditions and summarised results of experiments on gravity reactions of hoppers, with small or no temperature differences.

Expt.	Date	Time	No. of hoppers used	No. of counts	Interval between counts (min.)	Vertical length of cage (cm.)	Temperatures, ° C.		Hopper distribution (totals)
							Near roof	Near floor	
1	9.iii.	Sunrise to sunset.	30	20	30–45	110	21.2 29.7 25.7	21.2 29.8 25.9	500-3-9-0-0-2-0-10
2	9.iii.	Sunrise to sunset.	30	20	30–45	110	21.3 29.6 26.0	21.6 30.5 26.2	469-2-6-2-2-1-12-48
3	10.iv.	09.00–19.50	20	7	60–90	110	31.2 32.0 23.2	31.6 32.5 24.0	112-7-3-4-2-1-3-8
4	2.iv.	Afternoon	12	8	30	50	32.0 30.2	32.0 30.2	49-39-7-7

midday (the maximum) and the last reading of the day. In 4 a cage only 40 cm. long was used, and distribution in this was noted only in 4 sets, on the side of the walls in each half, on the floor and roof. Light intensity in the darkened tent where this experiment was made was too low for the exposure meter, but there was no apparent difference in vertical or horizontal illumination of the cage.

In 4 there was little temperature difference between the two ends; in 1, 2 and 3 small differences were shown by the thermometers. In the horizontal position the hopper is able to absorb a maximum of the sun's radiation during most of the day and the roof and floor of the cage were the only places where such position could be assumed. Even with hoppers crowding the tops of the cages very few hung upside down, whereas they usually sat horizontally on the floor. In 1, 2 and 3 the difference in body temperature on the floor and on the roof was probably greater than indicated. Even in 2 and 3 with the cage on the ground, differences were still less than temperature differences at similar levels in millet cultivation, for wind eddied round the screen.

Despite this difference, the great majority were at the top of a cage at all times, suggesting that the morning and post-meridional descents noted in the field were not due to a reversal or disappearance of geotaxis in connection with either high general temperature or high illumination intensity, such as obtain when the descents occur in the field.

There is no evidence that higher intensity of downwardly-directed light was responsible for bringing the hoppers to the top of the cage in experiments 1, 2 and 3. As shown above (p. 493) phototaxis may disappear or possibly become negative under such exposed conditions. In any case the majority were in the upper half also in 4, where light intensities were not appreciably different.

An observation comparable to 4 was made on 1st and 2nd instar gregarious hoppers in a breeding cage 60 cm. high. 2.iii. was a dark night with no moon or stars. Examined with a torch at midnight nearly all hoppers were found crowded along the upper edges of the wire-gauze walls and some on the roof. Temperature of the air at the top was less than 0.5°C . higher than immediately over the sand on the floor. Violent jarring brought hoppers to the floor, and the torch was extinguished. Inspected after 10 minutes all were again close to the roof. Repetition 5 times gave identical results.

In other observations an approximation to temperature conditions in the field was arranged. Cages were 30 cm. high by 15 by 30 cm., fitted with glass walls, a wire-gauze roof and floor. The larger floor area, lesser height and better protection increased effective temperature differences between the top and bottom of these cages as compared to the longer cylinders. The lesser height meant a smaller movement carrying the hopper to the floor, where a better position for maximum absorption of radiation could be assumed. Cages were in the open behind the windscreen. The hoppers were 5th instar indigenous ones and the cages inverted after each reading. The results are in Table XXVII, distribution being expressed as numbers in the upper and lower halves. Five were added to each cage after the 09.10 reading on 13.iii. and four after the 23.00 reading.

Here, where behaviour resembled that in the field, a conflict between reactions to gravity and temperature was evident. At night when vertical temperature differences were small, most hoppers were in the upper half, in daytime they were evenly distributed or in a majority on the floor, except midday on 14.iii., when temperature on the floor in the ground cage was over 40°C . and hoppers climbed off the ground to cooler levels, as they do in the field. The greater number found at the bottom in 2 as compared with 1 in Table XXVI seemed connected with temperature interferences in the same way. Hoppers were not at the bottom in early morning and evening, but during the day, when appreciable difference was recorded by thermometers in cage 2.

The same interference between temperature and gravity was striking in

TABLE XXVII.

Conditions and detailed results of experiments on gravity reactions of hoppers, with temperature differences during the day.

Date	Time	Cage on ground				Cage 1.2 m. off ground			
		Temp. near roof, ° C.	Temp. near floor, ° C.	No. upper half	No. lower half	Temp. near roof, ° C.	Temp. near floor, ° C.	No. upper half	No. lower half
12.iii.	23.30	24.3	24.4	13	2	24.3	24.3	11	4
13.iii.	06.45	24.7	25.0	10	5	24.8	24.8	13	2
	09.10	26.8	27.2	8	7	26.7	26.5	7	8
	13.30	31.5	32.2	5	15	30.8	31.3	4	16
	18.00	25.8	26.0	9	8	25.6	25.8	8	9
	23.00	25.0	25.2	11	5	24.8	25.0	12	5
14.iii.	10.00	33.5	35.5	2	17	32.9	32.9	6	14
	12.00	38.4	41.5	11	8	36.2	36.5	14	6
	14.00	34.0	36.6	8	11	33.0	32.8	10	8
	16.15	28.9	29.8	9	9	28.5	28.9	7	10
	18.05	26.7	26.7	10	8	26.5	26.5	8	9
	21.15	23.8	24.3	12	6	23.3	23.6	10	7

experiments on temperature reactions described below. Ten hoppers in a cylindrical cage, 20 cm. high, on a table, were subjected to alternating periods of 30 minutes in the sun and shade. After shading all were found near the top; on exposure to the sun, a vertical temperature gradient was set up and 2-5 hoppers settled on the floor. This alternation was consistent throughout the experiments. In sun and shade, maximum illumination came from above.

Comparison of these results with those in the longer cages, where temperature differences were less, shows how these can suppress geotactic responses, which can only come into play when the temperature differences are small, or when the lower positions are too hot. When, however, temperature differences are small, negative geotaxis may be very powerful.

Experiments to demonstrate geotactic reaction have not been made by others. Nevertheless it is true, as Husain and Mathur (1936) say, that "it is a matter of common observation that these [Desert Locust] hoppers when placed in breeding cages mostly remain near the top of the cage and near the source of light. They also show a tendency to keep their heads pointed away from the ground." Grassé (1923) found that *A. aegyptium* adults took a sloping path to light from the side, which he attributed to interference of geotaxis in the phototactic response he was studying.

The tendency of gregarious hoppers to face upwards in the field at night has been remarked particularly by Fraenkel (1929) and Williams (1933), the latter regarding it as the dominant feature of evening behaviour, to which both ascents and descents were subservient. In the assumption of a vertical position following a descent, mentioned by Williams, the descent was into animal burrows with air temperature probably higher than outside and the explanation of the descent as "in order to get into a vertical position, head upward, on the sides of the opening" seems hardly justified.

Field evidence for negative geotaxis has been adduced for cases of evening ascent before the occurrence of inversion of temperatures, where authors are

satisfied that positive phototaxis could not be effective (Fraenkel, 1929 : Lépiney, 1930a). Lépiney (*loc. cit.*) considered negative geotaxis as always latent in hoppers and as the dominant reaction in adults (1930d) when temperature is not high enough for band formation, jumping and flying, and I agree with this, but would emphasise the effect of temperature differences as well as absolute temperature level. Zakharov (1930) suggested geotaxis in ascents observed before temperature inversion, but attributed more influence to light. Smee (1936) mentioned geotaxis in relation to ascent in *Nomadacris*, but other factors are even less certainly excluded.

On the whole, there is evidence that negative geotaxis is always latent and sometimes becomes very strong.

(iii) *Temperature.*

In view of behaviour of hoppers in millet and the patchy temperature "field" in which they moved in daytime it is unlikely that either a directed reaction (topotaxis) or an avoiding reaction (phobotaxis) is most important in responses of hoppers to temperature, although they play a certain part (see Appendix 3). As already indicated, in millet the temperature field is very complicated, gradients are variable in steepness and run in all directions, so that the sustained reaction to a gradient implied by topotaxis is unlikely to assist in bringing hoppers to basking-places, for instance. There seems more scope for the operation of an avoiding reaction against lower or very high temperatures, but such reactions were seldom observed. Hoppers leaving a basking-place did not hesitate or turn back on reaching the edge of shadow. The only circumstance where avoiding reactions were apparent was in gregarious hoppers among shadows cast by leaves (p. 518).

While avoiding reactions may play a part, the cause of most hoppers being in basking-places was not the repeated avoidance of the borders, but the fact that once there they assumed the quiescent appearance described. Unless it be proved, however, that they are more active outside the basking-places, such negatively thermokinetic reaction cannot be claimed as the cause of basking and group formation. This could not be proved in the field (but see p. 518), but the following observation was made repeatedly. If the observer let his shadow fall over a basking group from a distance there was no immediate response due to visual disturbance, but after a minute or so they began to stir and the group gradually broke up, most hoppers climbing near-by vegetation. Here there was no temperature inversion and movement apparently was due to activation by a temperature decrease, that is, negative thermokinesis.

In the laboratory, however, Bodenheimer (1929), Parker (1930), and Hussein (1937) have demonstrated that locusts, like most poikilotherms, become progressively more active when subject to rising temperature, to the point of heat stupor; they are positively thermokinetic up to this point. That basking and group formation are not connected with heat stupor is apparent from the temperature level at which these phenomena occur and the highly responsive state in which hoppers remain.

Negative thermokinesis as a cause of basking contradicts positive thermokinesis found in the laboratory, but there are two differences in the application of temperature stimulus in the field, and the laboratory experiments: (i) the higher rate of change of temperature for active hoppers in the field; (ii) the action of irradiation and of convection and conduction.

Experiments were made with rapid temperature changes effected by sudden exposure to, and shading from, the sun. Part of the apparatus is shown in

pl. 9, fig. 18. Two wire-gauze cylinders 20 cm. high and 10 cm. in diameter were placed in shelter of a windscreen on a table in the open. A larger screen was hinged in front of the cages, which could be raised to shade, or lowered to expose, the cages. In one cage were 10 indigenous 5th instar hoppers, green with no black, in the other a similar hopper was impaled on the thermocouple needle fixed horizontally. Alongside the impaled hopper was a plain and a black-bulb thermometer.

After an hour simultaneous readings were taken, at one-minute intervals, of the body temperature of the impaled hopper, the temperature of the two

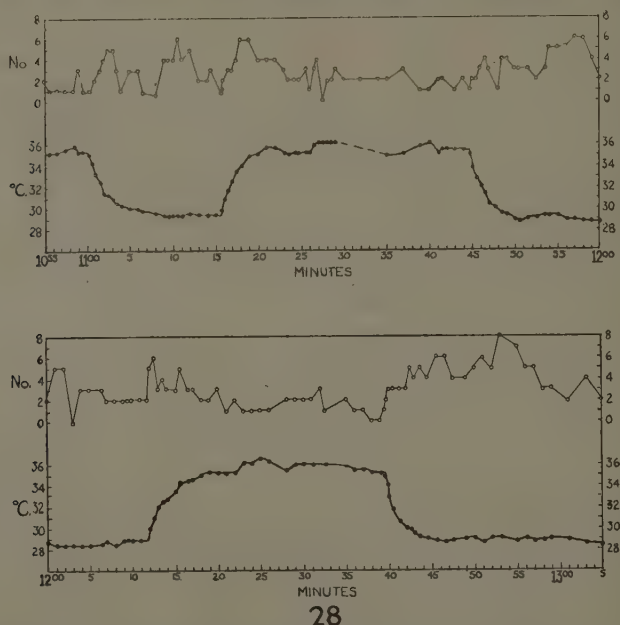


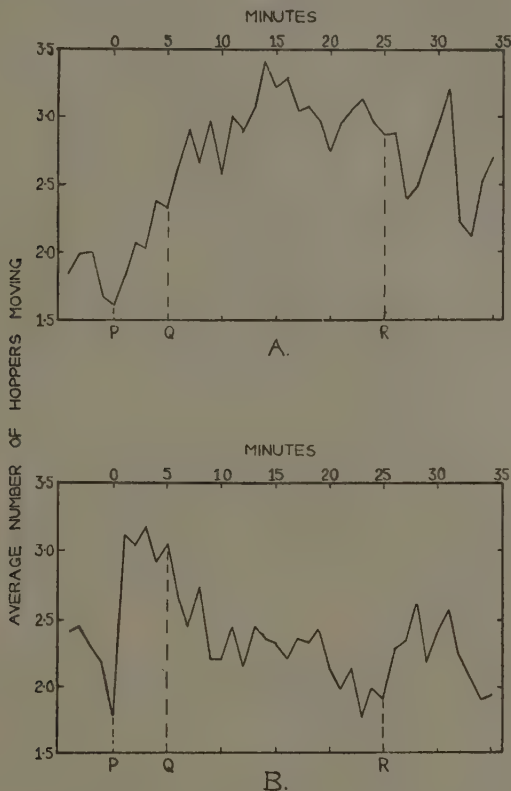
FIG. 28.—Sample record from experiments on the effect of temperature changes on hopper activity. Thin line above indicates number of hoppers moving; thick line below indicates internal body temperature of a fixed hopper.

thermometers and the number of hoppers moving in the other cage. The observer's small movements were visible to the hoppers, but were carried on the same way throughout the experiments, and the hoppers seemed unaffected. Readings were usually taken for 30–40 minutes with the screen up and then with it down and so on. They were kept up for 5 hours on 4 days, totalling 17 exposures in each condition. Half-way through, the table was moved to compensate for the sun's movement and the wind direction changing from north to north-east or east, which two events fortunately were concurrent.

The screen behind the cages only prevented a direct flow of wind, and not the free circulation of air. An Edney paper hygrometer under a wooden shade showed changes of 1% or 2% relative humidity when the screen was raised or lowered, and humidity may be considered controlled in the experiments.

Raising or lowering the screen produced an unavoidable change in light intensity and light was uncontrolled, except partially, inasmuch as field behaviour is not consistent with reactions to light predominating, as mentioned above. The time relations of responses (figs. 28, 29, 30) also suggest temperature rather than light as the operative stimulus.

Neither sun nor shade temperature, nor their difference, could be maintained



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FIG. 29.—Averaged results of all experiments on the effect of temperature changes on hopper activity. A. Effect of a temperature decrease; B. Effect of a temperature increase. Further explanation in text.

constant throughout the experiments, but they were made well after sunrise and well before sunset on each day. On 18.iii. the change in body temperature on exposure to, or shading from, the sun varied from between 29–36° C. to 28–32° C.; on 19.iii. from 29–39° C. to 29–34° C., on 20.iii. from 30–39° C. to 30–36° C.; and on 21.iii. from 26–32° C. to 31–39° C.

A sample of the results is shown in fig. 28; the rate of change of temperature was rapid, usually 5° in the first minute, slowing down to reach a new steady state after about five minutes. Fig. 28 also shows at their “best” the changes

in activity level (number of hoppers moving out of 10) associated with the changes in body temperature. Exposure to the sun produced in a few seconds an increase of activity. This began before body temperature had reached a new steady state but was short-lived, and it often consisted only in the movement of hoppers at the top of the cage which brought a few to the floor where, after a minute or two, during which the body temperature of the impaled hopper became steady, they became quiescent, often with bodies broadside to the sun. Relative quiescence continued for 20-25 minutes, with sometimes slight return to activity towards the end. When the screen was raised to shade the cages, body temperature of the impaled hopper fell rapidly, but no immediate response was observed. In the next 5-10 minutes the free hoppers began to move until 5 or more were moving at once; this activity was sustained for many minutes. Usually it decreased again, after 20-25 minutes from raising the screen, but sometimes remained fairly high until the screen was again lowered.

The experiments are averaged in fig. 29, ignoring differences in temperature and activity levels. For 17 cases in each condition the average number moving each minute is plotted for 5 minutes before raising the screen (*P* in fig. 29, A) or lowering it (*P* in fig. 29, B) and for 35 minutes afterwards. The figures illustrate clearly the relation described above. The decrease in activity in the 5 minutes before the change of exposure (particularly in fig. 29, B) is due to changes of exposure probably coming too close in time to permit an adapted activity level to be reached.

The changes in average activity level are small, and averaging without taking

TABLE XXVIII.

Summarised results of experiments on the effect of sudden temperature changes on locomotor activity of hoppers.

Date	6-25 minutes (inclusive) after temp. rise		6-25 minutes (inclusive) after temp. fall		Difference ($Y - X$)
	Period no.	Av. no. of hoppers moving per minute (X)	Period no.	Av. no. of hoppers moving per minute (Y)	
18.iii.	1	2.3	2	3.4	+1.1
	3	1.7	4	4.7	+3.0
	5	1.8	6	3.0	+1.2
19.iii.	1	2.7	2	4.1	+1.4
	3	3.1	4	3.1	0.0
	5	3.1	6	2.3	-0.8
20.iii.	7	2.0	8	2.7	-0.7
	1	1.1	2	3.4	+2.3
	3	2.5	4	3.7	+1.2
21.iii.	5	1.7	6	3.5	+1.8
	7	4.5	8	3.6	-0.9
	9	3.7	10	3.3	-0.4
	1	0.4	2	0.8	+0.4
	3	1.8	4	2.1	+0.3
	5	1.9	6	2.7	+0.8
	7	1.7	8	3.5	+1.8
	9	0.5	10	0.7	+0.2
Total 17			Total 17		Mean +0.83

account of differences in general activity level at different times, reduces the apparent strength of the response. The difference in levels between points *Q* and *R* in A and B is statistically significant. Table XXVIII shows the average number of hoppers active per minute in the 20-minute period between *Q* and *R* (including *R*) in fig. 29: that is, 6–25 minutes after change of exposure. The first 5 minutes is omitted to avoid the initial outburst of activity after an increase of temperature. This is justified below. The "period numbers" indicate the chronological order of alternate exposures on each day. Each 20-minute period after a temperature rise is compared with a 20-minute period after a subsequent fall and the difference given in the final column. The average difference is 0.83, standard deviation of 1.07 and standard error 0.26. The difference would occur by chance between 9 and 3.2 per mille and is significant.

Thus, ignoring the uncontrolled factor of light, there is a negative thermokinesis in hoppers under special conditions of heating by radiation and of rapid temperature change. These conditions are maintained in the field most of the time hoppers are active and behaviour seems correlated with temperature distribution.

The size of difference in activity levels after a rise or fall in temperature obtained in the experiments, is not a good indication of the size in the field. The increase after shading was considerably less in the cages than in the field and is probably connected with the inhibitory effect of the cage walls. Similarly a hopper on increasing its temperature, by passing from shade or down from a millet stand to a basking-place, made only small movements before quiescence, but in the cage most were hanging vertically near the top when temperature increased, and more movement was observed before they settled down again. This difference is probably connected with the orientation reaction to radiant heat demonstrated by Fraenkel (1930) and apparently present, although less conspicuous, in solitaries. In the field a hopper was already in a horizontal position on coming to a basking-place and its orientation reaction could be completed quickly with a minimum of locomotion; this was not so in the cage.

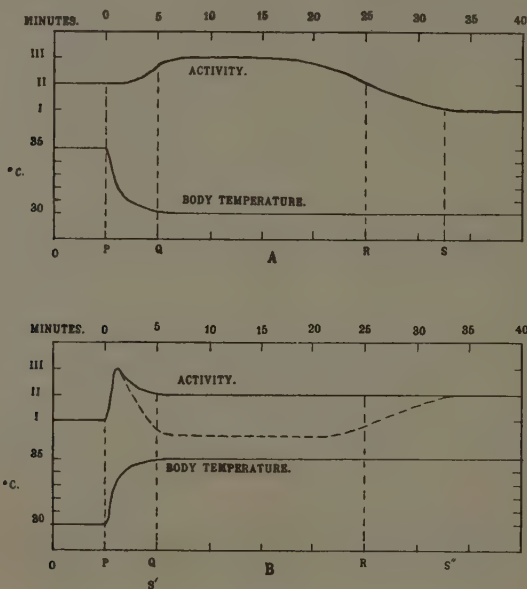
Differences in the time relations of the initial outburst of activity after a temperature rise, before body temperature became steady, and the slowly appearing but sustained activity after a fall, occurring principally after the steadying of internal body temperature, suggested that perhaps two responses were concerned, one acting through surface receptors, the other, negative thermokinesis proper, through more deeply seated ones. On these grounds the initial outburst after temperature rise was omitted in calculating differences in Table XXVIII. In natural conditions this outburst probably represents "fidgeting" (see p. 465) of the orientation reaction which would not prevent negative thermokinesis from keeping hoppers quiet on the basking-places and moving elsewhere.

Hoppers were not seen to remain on a basking-place for hours at a time and, had activity risen again after 20 minutes as in the experiments, the relative quiescence during that period would be consistent with field behaviour. In the field a hopper usually found another basking-place if it kept moving for several minutes, and again became quiescent, so that as a whole they spend most of their time basking.

Negative thermokinesis may be a special reaction to heating by radiation, or related to rate of temperature change, and yet be reconciled with laboratory findings of positive thermokinesis, with slower temperature change. In

Parker's experiments (1930, on *Melanoplus mexicanus mexicanus* Sauss. and *Camnula pellucida* Scudd.) air temperature in the chambers rose $1^{\circ}\text{C}.$ in 5 minutes; in Bodenheimer's (1929, on *Schistocerca*) by $1^{\circ}\text{C}.$ in 6 minutes; and in Hussein's (1937, on *Schistocerca*, *Nomadacris* and *Locusta*) rose by $1^{\circ}\text{C}.$ in 5 minutes and fell $1^{\circ}\text{C}.$ in 8 minutes; in my experiments it rose and fell initially by $1^{\circ}\text{C}.$ in 10–15 seconds.

It is quite certain that positive thermokinesis operated in the field. In general, despite intermittent periods of quiescence, hoppers were not only more excitable but also more active at higher screen temperatures, and it is suggested



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FIG. 30.—Idealised curves expressing the effect of temperature changes on locust activity. Further explanation in text.

that negative thermokinesis is not in contradiction to, but simply overlays, positive thermokinesis in insects moving in a close patchwork of temperature and thus subjected to rapid and frequent temperature changes.

Had hoppers been left at a constant temperature after changes such as those in the experiments, the adapted activity level associated with that temperature must have been reached eventually, perhaps as in fig. 30. No data were available to show the true adapted activity level at any temperature as compared with levels shortly after changes, so that fig. 30 is hypothetical. In it the onset of a change in body temperature of $5^{\circ}\text{C}.$ is assumed to occur at P. In A activity prior to P is at level II, the adapted level corresponding to $35^{\circ}\text{C}.$ In the 5 minutes after P body temperature falls to its new steady level at $30^{\circ}\text{C}.$ and activity increases to level III, gradually falling to its new adapted level I

(corresponding to body temperature of $30^{\circ}\text{C}.$) at *S*, 25–30 minutes after the onset of change. In *B*, activity before the change is at adapted level I (corresponding to body temperature of $30^{\circ}\text{C}.$). Body temperature begins to rise at *P* and an immediate increase of activity up to level III occurs, but it falls quickly to the new higher adapted level II (corresponding to $35^{\circ}\text{C}.$) at *S*¹, 5–10 minutes after the onset of change. The true condition in *B* may be represented by the broken curve, where activity falls below level I, the new level II being reached only at *S*¹¹, 25–30 minutes after the change.

Fig. 31, based on Bodenheimer, Parker and Hussein, represents the hypothetical normal relation of slowly changing temperature to activity. No scale can be inserted on the vertical axis as the authors divide activity into arbitrary grades; the curve is therefore provisional. Figs. 30 and 31 considered

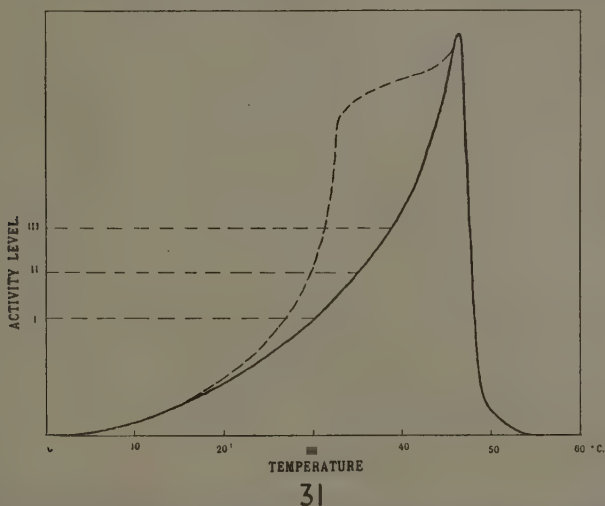


FIG. 31.—Hypothetical curve of changes in activity level under the influence of slow-temperature change. Thick continuous line, *ph. solitaria*; thin broken line, *ph. gregaria*. Further explanation in text.

together suggest an explanation of behaviour at midday on hot days: cessation of basking, break up of groups and retiring to cooler positions. Activity levels I, II and III in fig. 31, representing adapted levels at 30° , 35° and $39^{\circ}\text{C}.$, respectively, correspond with similar levels in fig. 30.

As regards temperature-behaviour relations at the upper end of temperature scale, investigators agree that when temperatures exceed $40^{\circ}\text{C}.$ "excitement" becomes evident,⁴ that is, the activity curve in fig. 31 steepens sharply. Even if relations between the two activity curves in fig. 30, *A* and *B* remained, only the section *P-Q* of curve *B* would operate since hoppers are too active at high temperatures to stay exposed long enough for the subsequent part to operate; this would result in disappearance of negative thermokinesis. Steepening of the adapted activity-temperature curve probably means that the activity level

⁴ The equation of sun temperature of $40^{\circ}\text{C}.$ with the same reading of air temperature in the laboratory is not as unjustified as appears owing to regulation of body temperature in the field at sun temperatures at about $40^{\circ}\text{C}.$ (see p. 477).

at any time after exposure to higher temperature would exceed greatly that at any time after entering a temperature below 40° C. Thus a strong positive thermokinesis would supervene, and this was observed in the field. The few hoppers on bare ground in the heat of the day always moved quickly until they reached a cooler situation.

The operation of negative thermokinesis is not apparent at the lower end of temperature scale in fig. 31, firstly because the insects do not move sufficiently to encounter temperature differences, secondly because changes have less effect at the lower end of the scale, and thirdly since with temperatures around 20° C. in the field differences were practically non-existent. As temperature gradually increased or decreased in activity changes would follow; that is, a weak positive thermokinesis, not affecting distribution, would be evident. This was observed in the field about sunrise and sunset, but there light was probably as important as temperature, if not more so.

It is concluded, therefore, that negative thermokinesis, on theoretical grounds, could only be the dominant reaction in the field between 20 and 40° C. Below 20° C. weak positive thermokinesis would appear and above 40° C. it would supervene strongly. This accords with field observations.

Zimin's description of behaviour of hoppers of *Calliptamus italicus* (1931) illustrates this. In the midday "retiring to shade," hoppers came out and stayed to feed on the ground in the sun, only to be activated again if their position became hot, and alternated thus between sun and shade (apparently activated by hunger in the shade) till falling temperature made it possible to abandon shade.

At Hamashiameb this reaction, however strong, was not predominant at the hot time of day. Hoppers kept strictly to cooler positions and ventured so very rarely to the hot ground that a more efficient reaction than a kinesis, e.g. an avoiding reaction, probably operated. Kinetic stimulus of the hot sand to the insects' tarsi also cannot be left out of account.

Negative thermokinesis is not claimed as the sole reaction concerned even in other phases of the diurnal regime. Considering the observed behaviour, negative thermokinesis, however, seems to occupy a considerable, if not a dominant, rôle.

Reactions to temperature have been more discussed in literature than any other aspect of behaviour; nevertheless the problem is still in an unsatisfactory and even confused state. Behaviour is often described as thermotactic or thermotropic when it may be thermokinetic (see p. 435).

Parker, Bodenheimer and Hussein (*loc. cit.*) have established a relation between temperature and stages in an arbitrary scale of activity. This is expressed in provisional form in fig. 31, but awaits quantitative statement, and the evidence for negative thermokinesis adduced above shows that fig. 31 represents only one aspect of the relation.

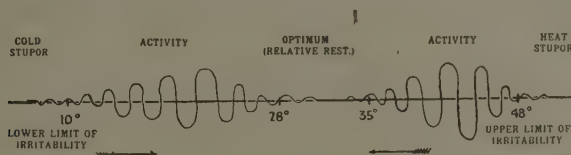
In an early detailed account (La Baume in Bücher, 1918) of morning and evening basking band formation by gregarious *D. maroccanus* the idea of negative thermokinesis was expressed: "... Empfinden die Heuschrecken wahrscheinlich die grössere Wärme solcher Stellen, wenn sie über dieselben hinkriechen, und werden dadurch *veranlasst, auf ihnen sitzen zu bleiben*" [my italics]. The meaning was somewhat obscured in Uvarov's (1928) description of La Baume's observation by the use of the word "thermotropism" (see Appendix 3). Fraenkel (1932) used similar terms to La Baume in discussing morning and evening band formation, as does Lépiney (1933). None of these observations constitutes proof of negative thermokinesis, and the hypothesis

has received little attention perhaps owing to the difficulty of conceiving that negative and positive thermokinesis are reconcilable.

Zakharov (1932) proposed a comprehensive "theory of migrations of the Migratory Locust" where movements are attributed to "dissatisfaction" of the insects with their state and an "inner physiological need" to change position, while optimum conditions are accompanied by the minimum of movement and in the ideal state by complete absence. Questionable as these assumptions may be, he recognises the necessity of accounting for the quiescence of "basking" individuals observed at intermediate temperatures which could not cause cold, or heat, stupor.

Fig. 32 is from Zakharov's paper and represents his conception of relation between temperature and activity. Instead of an activity curve rising to heat stupor, there is an inactive period between 28° C. and 38° C., when "optimum" conditions prevail and the insects while inactive remain capable of immediate reaction to external stimulus (a common observation).

This hypothesis, while recognising the problem, appears misleading and does not help in solution. If relation of temperature to activity is considered physiologically, there is no "optimum" where temperature is intermediate and activity at a low level as experiments have shown (fig. 31). In the field



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FIG. 32.—Relation between temperature and activity according to Zakharov (1932).

there is an apparent period of "relative rest." This may be illusory, for individuals basking on bare ground are the most conspicuous of a (solitary) population; if it represents reality it is related to the existence of spatial temperature differences, just as collection in a "preferred" region of a temperature gradient in the laboratory is associated with temperature differences. These differences repeatedly subject active hoppers to the negatively thermokinetic effect of temperature changes. "Optimum" might be used as a synonym for "relative rest," but Zakharov makes it the cause of the "relative rest" without evidence. Similar arguments can be advanced for gregarious hoppers. Thus, while fig. 32 may represent the apparent or effective condition in the field, it does not explain the relation between temperature and activity.

Mention may be made of the work of Nicholson (1934) on influence of temperature on activity of blow-flies and his review of the relevant literature. He notes that "activity is a complex phenomenon, and that the character of the results obtained is influenced by the kind of activity examined, by the methods of measurement used, and by the nature of the temperature conditions to which the insects are exposed." Nicholson obtained a curve (fig. 8) of flight activity against temperature which resembles fig. 31, when temperature was rising about 1° C. in 8 minutes, but when temperature was kept constant for many hours maximum activity occurred at the middle of the range, and

was very low at the temperature of maximum ("distress") activity with rising temperature.⁵ Weber (1931) also obtained a curve very like fig. 31, for the thermokinesis of *Trialeurodes vaporariorum* (Westw.).

Parker (1924), Bodenheimer and Segal (in Bodenheimer, 1929) and Rubtzov (1935a) made "temperature preference" experiments on Acridids. In none were convection currents or humidity satisfactorily controlled, nor, in Parker's and Bodenheimer's, any attempt made to ensure that air temperature at a given position was the same as that of the surface on which the insects rested. In Parker's experiments, with unenclosed apparatus, humidity differences were probably small but light was not controlled. He used a glass plate heated in the centre by electric light below, and found young hoppers of *Camnula pellucida* came to rest after several hours in a ring round the lamp where temperature was 36–38° C. He says, that owing to possible interference by positive phototaxis the experiments show only that temperatures above 38° C. are avoided, and do not prove that those below 36° C. are avoided. Bodenheimer and Segal, with gregarious *Schistocerca*, used a "Temperaturorgel" designed by Herter and criticised by Gunn (1934). Larger insects were unable to turn round in it. Results showed considerable scatter about the means, which rose from 27 to 29° C. for 1st instar to 37° C. in 5th instar hoppers and 39° C. in young adults. Preferred temperature for 1st instar gregarious *Schistocerca* is much lower than that at which similar hoppers remained basking at Hamashiameb (see p. 520). Rubtzov, working with various Siberian Acridids, principally *Chorthippus albomarginatus* (De G.) and *Omocestus haemorrhoidalis* Chap., used an improved gradient in which differences of temperature of the floor and the air were probably less than in the Herter type used by Bodenheimer. Attempt was also made to study the interaction of humidity and temperature gradients present in such apparatus. A drying agent was put in the cold end and wet cotton wool in the warm end overnight. It is not clear whether they were removed before experimenting, and humidities were not measured. Rubtzov is convinced his results show only a minor reaction to temperature, but a strong one to humidity, the insects preferring moist to dry air.

Such temperature preference experiments indicate what to look for in the field or in further experiments, but since they leave the mechanism of the response unanalysed, results cannot be transferred directly to explain behaviour in the field, without certainty that the temperature stimulus is applied in the same manner (see p. 533).

Grassé's simple experiments on temperature reactions of Acridids (1922) remain in some ways the most satisfactory. He observed *Anacridium aegyptium* singly in a wire-netting cylinder facing a warmed plate at one end, the whole being in semi-darkness. When the plate was below 40° C. insects advanced from the opposite end and, apparently, sat quiet near the plate with bodies parallel to it. The paths of the insects were never rectilinear, but always more or less towards the plate, so the reaction seems not a matter of trial and error; topotaxis was probably at work. It is not clear that relative inactivation (negative thermokinesis) was observed near the plate, or whether insects were reacting to radiant heat or to a gradient of air temperature in the cage. The former alternative might be favoured as there is no evidence that they direct their antennae to the source of warmth, shown by Wigglesworth and Gillett

⁵ Sioli (1937) records a sudden exposure to a not unfavourable strength of radiant heat causing a walking bed-bug (*Cimex lectularius*) to halt for a few moments. I know of no other account of negative thermokinesis in insects.

(1934) to be an essential part of the telotactic response of *Rhodnius prolixus* to gentle gradients of air temperature (see Appendix 3).

When Grassé's plate was heated over 40° C. insects were attracted, but after a few minutes moved away to return later and repeat the cycle. Both positive thermokinesis and reversal of thermotaxis from positive to negative are evident.

The above evidence shows how complex is the relation of temperature to behaviour and that, with a patchy temperature field, the effects of general temperature on activity level or on responses to other stimuli constitute only one aspect of the complete relation.

(iv) Summary.

1. Hoppers and adults are positively phototactic at low or moderate intensities of illumination (below 1000 metre-candles) if they are not too active.

2. If activity is increased by bright illumination or higher temperature etc., positive phototaxis probably disappears, but it possibly reverses to negative under bright illumination.

3. Positive photokinesis is probably latent at all light intensities.

4. Negative geotaxis is latent at all light intensities and temperatures, but may be easily suppressed, for example by temperature reactions.

5. Positive thermokinesis is latent at all temperatures up to heat stupor and probably dominant at low and high temperatures in the field.

6. At intermediate temperatures positive thermokinesis can be overlaid by a negative thermokinesis associated in the field with rapid temperature changes undergone by the active insects, and perhaps connected with heating by irradiation.

7. Thermophobotaxis, not investigated experimentally, was not evident in solitaries in the field.

8. Thermotopotaxis, demonstrated in *A. aegyptium*, is thought unable to play a large part in nature, except possibly in morning and post-meridional descents.

4. Conclusions on the controlling factors in the diurnal behaviour of older hoppers in unweeded millet.

On the basis of preceding sections tentative conclusions may be drawn on the controlling factors at work in diurnal activity.

1. Beginning and ending of activity.—These are kinetic phenomena unconnected with changes in distribution. Activity commenced in the field at a variety of temperatures (20–25° C.) and ended at a variety of higher ones (25–29° C.), all being above those associated in the laboratory with Hussein's (1937) "activity depressed by cold" (13–22° C. in 5th instar *Schistocerca*). Field and laboratory phenomena are not comparable and the same type of thermokinesis cannot be at work in both situations. When activity begins in the field temperatures are beginning to rise; when it ceases the rate of temperature fall is decreasing markedly. Unless the beginning and ending of activity are regarded as related to these particular types of temperature change, the light factor, in the form of photokinesis, must be allotted the major rôle in these phenomena, since their relation to light intensity is fairly consistent.

2. Morning ascent and exposure of bodies to sun.—Negative geotaxis alone would account for direction of ascent, temperature differences being small. The increase of activity involved in the ascent may be attributed to increasing

illumination (positive photokinesis) and rising temperature (positive thermokinesis). Activity and vertical light intensity being still fairly low, positive phototaxis may assist the ascent. Exposure to the sun is at first probably due to light, but body temperature is soon higher in the sun than in the shade so that a temperature reaction (phobotaxis or negative thermokinesis) is probably involved.

3. Morning descent.—Activity continues to increase, now probably due more to positive thermokinesis than photokinesis, as light intensity increases less rapidly. Increased activity alone must contribute much to removing the bulk of hoppers from the tops of the millet and bringing some to the lowest levels. The movements in this phase are random and only result in a general descent because fewer re-ascents than descents are made. Mechanical and thermal effects of the rising wind probably help to drive hoppers down from the upper levels. Significant vertical temperature differences appear and the temperature reactions associated with basking suppress negative geotaxis. Positive phototaxis probably also disappears with increased activity and illumination, but phototaxis may become negative and assist in descent. The descents may be partly assisted by positive thermotopotaxis, for they proceed along a definite temperature gradient.

4. Basking and group formation.—With small patches of bare ground becoming the warmest positions, temperature reactions override all others. Hoppers collect on the patches as a result of negative thermokinesis. Avoiding reactions against cooler situations may assist group formation. The rôle of thermotopotaxis remains obscure and temperature gradients on the ground are so confused that it does not appear that it could be great. Groups are formed not as a result of gregariousness but because the number of bare patches is limited in relation to number of hoppers in the vicinity. Where wind currents penetrate cultivation they play a part in further limiting the area available for basking.

5. Midday break-up of groups, retiring to cooler situations, and ascent.—The basking-place temperature now reaches a point where strong positive thermokinesis supervenes, hoppers are unable to remain quiescent and settle in cooler places. Thermophobotaxis prevents, except rarely, their re-entry to the hot places. Of the available cooler places, negative geotaxis is responsible for those on the millet stands being preferred to shaded positions on the ground. It is also probably responsible for hoppers climbing to cooler positions than those in which they had basked on the ground. Cooler positions are not restricted and hoppers do not remain grouped at this time.

6. Afternoon descent, resumption of basking, re-formation of groups.—As soon as ground temperatures fall to a level where negative thermokinesis can take effect, and the warmer ground positions are no longer avoided phobotactically, basking and group formation starts again, for reasons given in 3 and 4 above.

7. Evening break-up of groups and ascent.—The groups break up, when they become shaded, by negative thermokinesis. Even if the basking situations remain slightly warmer than neighbouring ones, the difference is too small to allow negative thermokinesis to keep new arrivals on the basking-places in opposition to negative geotaxis, and towards the end, positive phototaxis. The latter is probably not concerned at the beginning of the phase which begins at from 1 to $3\frac{1}{2}$ hours before sunset. Sunny positions high in the millet are warmer than shaded ones below, and thermophobotaxis, and possibly thermokinesis, help to keep hoppers in exposed positions, and in any well-blanketed ones, inside bushes, etc., where air temperature is $1-2^{\circ}$

higher than elsewhere. Exposure of bodies to the sun, when radiation is weak, is probably connected with light as in the morning ascent.

Phases of diurnal behaviour depend on many interacting components, separation of which is always an abstraction (Strelnikov 1936a). The omission of humidity in the above analysis, for instance, does not exclude it from a conditioning rôle. Nevertheless, it is permissible to indicate which components seem decisive in each phase; these are set out in Table XXIX.

TABLE XXIX.

Suggested scheme of operative components in various phases of the diurnal behaviour routine of older hoppers in unweeded millet cultivation. For explanation of terms see Appendix 3.

Behaviour	Principal components	Accessory components
Beginning and ending of activity.	Pos. photokinesis.	Pos. thermokinesis.
Early morning increase, late afternoon decrease, of activity.	Pos. photokinesis. Pos. thermokinesis.	
Mid-morning increase, mid-afternoon decrease, of activity.	Pos. thermokinesis.	Pos. photokinesis.
Morning and evening ascents.	Neg. geotaxis.	Pos. phototaxis.
Midday ascent.	Neg. geotaxis.	
Morning and evening exposure to sun.	Pos. phototaxis.	Neg. thermokinesis. Thermophobotaxis (avoidance of cooler).
Morning and afternoon descents.	Pos. anemokinesis. Anemophobotaxis (avoidance of windier). Neg. thermokinesis.	Thermophobotaxis (avoidance of cooler). Pos. thermotopotaxis. ? Neg. phototaxis.
Basking on ground (and group formation).	Neg. thermokinesis.	Thermophobotaxis (avoidance of cooler). Pos. anemokinesis. Anemophobotaxis (avoidance of windier). ? Pos. thermotopotaxis.
Midday cessation of basking (break-up of groups).	Pos. thermokinesis.	
Evening cessation of basking (break-up of groups).	Neg. thermokinesis.	Neg. geotaxis. Pos. phototaxis.
Midday keeping to cooler places.	Thermophobotaxis (avoidance of warmer).	Pos. thermokinesis. ? Neg. thermotopotaxis.

5. Daily behaviour of older hoppers in other vegetation zones.

In unweeded millet, behaviour was dependent on the patchy nature of the temperature field. The virtual absence of wind not only allowed the sun

to produce this, in conjunction with dense irregular vegetation, but also left hoppers mostly undisturbed.

Other zones differed from unweeded millet in exactly these two characteristics, since they had less dense and less irregular vegetation and were penetrated more by wind. Hence, while the temperature field in other zones was not studied closely, it was not surprising to find clear definition of the various phases of daily routine lacking.

At the other extreme of density and wind shelter, in the open plain, Ia, and the sand dunes, Ib, diurnal behaviour was studied in the 3-day wandering experiments (see pp. 422-427). It was found that behaviour was radically different from that in unweeded cultivation. There was no clear sequence of phases, except in so far as movement ceased some time before sunset, and it was expected that with high temperatures at midday (which did not occur when indigenous hoppers were present at Hamashameb) hoppers would be found on vegetation. Basking on the ground was unusual, and hoppers on the ground usually wandered and only remained still for long periods when on vegetation. Behaviour was thus not closely related to temperature, except that on bushes hoppers tended to spend most time in sunny sheltered positions. Aggregation was in any case out of the question owing to paucity of hoppers.

Behaviour in zone II, continuous dense grass, was noted in the Trench Experiments (pp. 415-417). There was a vertical temperature gradient in the day running from top to bottom of the grass (fig. 14 and p. 471). Near sunset this became inverted, and behaviour seemed correlated with these gradients. Before sunrise no hopper was seen, but shortly after they began to appear among the grass tops and, if the wind was not strong and the day not hot, they remained here until sunset, when they again descended to the bottom. If a strong wind blew at any time of the day they descended, presumably because air temperature was always higher under than over grass and body temperature would only be much higher among the tops if the wind was not strong, and because of the mechanically stimulating effect of the wind. Similarly on hot days, even with no strong wind, they went down into the shade of the grass, presumably because at the top their bodies reached the critical temperature at which thermophobotaxis and thermokinesis reverse, and their bodies would be cooler in the shade. Behaviour, including vertical movements, appeared, therefore, more closely related to temperature in this zone than in the concentration zone. Closely similar behaviour of gregarious hoppers of *Locusta* is recorded by Allan (1933), who compared diurnal routines in millet and eight-foot dense grass, and showed that differences were associated with temperature distribution in the two types of vegetation. Despite the presence of numerous hoppers of all ages, group formation was neither expected nor found in dense continuous grass, since the horizontal temperature field is fairly uniform and the external causes of aggregation in unweeded millet lacking.

Behaviour in grass interspersed with bare patches was not followed all day, but basking groups were noticed on the patches (Table VI), or the lee edges of dense grass. Here the horizontal temperature field is much more patchy than in continuous grass, and the bare ground well sheltered from wind, so group formation was expected.

The *H. undulatum* mats among the dunes had a good population of young hoppers, but not so many 4th and 5th instar hoppers. Micro-climatically they vary in the direction either of dense grass or of grass with bare patches, depending on the density of the mat. However dense the mat, bare ground is always available within a metre, which is not always the case in dense grass.

Attempts to observe all-day behaviour on the mats were unsuccessful owing to the difficulty of seeing without disturbing the hoppers. On the basis of separate observations it seems that the older hoppers spend the night on the stems and descend to sit in sheltered sunny positions most of the day, sometimes forming small groups, and ascending in the evening. There is some evidence of a midday ascent on hot days. Formation of groups was noticed under the lee edge of the mats, the only place where much bare, sheltered and sunny ground was available. It was not apparent why some hoppers were in groups and not uniformly scattered along the edge, but small local air currents probably played a part here as on other basking-places (see p. 485).

Zone III, irregular low vegetation, was of variable density and wind-breaking properties. It resembled dense grass with bare patches, but wind shelter was much less complete on the ground, and taller vegetation (*Suaeda*) was present. Diurnal behaviour was not studied closely. Basking individuals and odd groups were often seen. The irregular vegetation, penetration by wind, and older hoppers tending to scatter from the zone, reduced chances of aggregation greatly where sharp differences in vegetation height were absent.

In many places, however, where *Suaeda* bushes stood out conspicuously from each other and from the undergrowth, each bush had a small concentration of older hoppers. A few were sometimes seen basking on the sunny lee side of the bare mound usually present at the base of each bush. Little aggregation was produced thus in most places, presumably because of the inadequate warmth and calm, but at one place at Wara Dibbab where discreteness and size of bushes and mounds was exceptional, aggregation was conspicuous. These mounds (pl. 4, fig. 7) are mentioned under Concentration (p. 409), but it should be added that groups of 10-40 hoppers were basking on the sunny lee side of each mound. Ground wind currents were clearly important in this aggregation.

Nevertheless, under better conditions, aggregation could be more persistent and might lead to gregarisation; this must be remembered when surveying possible outbreak centres without millet.

In IVa, *Suaeda* bushes and undergrowth similar to IVc, behaviour was little studied, but it is supposed to be as in unweeded millet, except that the evening ascent would be dominated by collection inside the warm interiors of the bushes. This zone could certainly produce aggregation and gregarisation, if ground vegetation did not dry too soon, and is also to be borne in mind.

In IVb, weedless millet, diurnal behaviour of indigenous hoppers was not observed, but extreme *dissocians* 5th instar hoppers were observed on 27.iii. (see p. 521 and figs. 35, 36). These behaved like older indigenous hoppers in unweeded millet, but were less numerous and their groups small. This may be due to the less patchy nature of the temperature field on the ground in weedless millet (fig. 15, C), for as many hoppers were basking singly as were in the small groups. That groups were formed at all may be due to vestiges of gregariousness or, more probably, to the effects of small local air currents, for groups were usually on the lee side of the stands. Local wind currents were not investigated in relation to these groups (see fig. 23), but cigarette-smoke trails showed the ground to be draughtier in clean than in unweeded millet.

6. Daily behaviour of younger hoppers, and of adults.

(i) Young hoppers.

Observations on 1st to 3rd instar hoppers were few. They were much less active than older hoppers and spent most of their time on ground

vegetation. On *H. undulatum* mats, locusts basking singly, or in groups, usually included some young hoppers, but in relation to those present the proportion was very small. Behaviour of young hoppers in unweeded millet was observed all day on 16.ii. Virtually none were found on the higher levels of the millet stands at any time. A very small proportion was basking when older hoppers and adults were doing so. Basking young hoppers kept noticeably even more closely to ground vegetation than older ones and were often right among the stem bases. They left the ground at midday but the exact time was not observed. The behaviour of 50 new-hatched hoppers, probably of *dissocians* phase, was observed on 27.iii. They remained on broken millet throughout the day, with no sign of primary band formation. When disturbed some hopped to the ground but immediately returned to millet stalks.

It is concluded that whether reactions to external stimuli, similar to those of older hoppers, are latent in young hoppers or not, they are too inactive and phytophilous to display a clear diurnal routine, and make a very small contribution to aggregation.

(ii) *Adults.*

The diurnal behaviour of adults in millet resembled that of older hoppers.

Differences existed, however, as may be seen from notes under fig. 10. When mass behaviour was observed all day, as on 16.ii. (fig. 10), adults appeared on basking-places 20-30 minutes before hoppers. Adults sat on the ground not only in places close to undergrowth but also away from vegetation on larger bare patches such as is shown in pl. 16, as well as outside the millet field in sheltered positions on the lee of mounds. Many more adults than hoppers basked singly because of this. Moreover, they were observed to remain long basking in one place unlike older hoppers. At the same time, the proportion of adults remaining all day on the millet was greater than that of the hoppers.

When sun temperature on bare sheltered ground reached 40° C., some adults climbed on the millet. Many, especially those outside the millet, remained on the ground, but moved to positions exposed to the wind. Thus for adults temperatures at E in fig. 10 must be included in "available temperatures." By moving to such positions many adults kept nearer to 40° C. than did the hoppers on the millet. On 27.iii. midday temperature rose higher than on 16.ii. (figs. 35, 36) and *dissocians* adults deserted even the windiest positions on the ground at midday, retiring to upper levels on millet.

Adults began the post-meridional descent and resumption of basking in sheltered ground positions somewhat before hoppers. Beginning and ending of activity and morning and evening ascents were almost simultaneous with those in hoppers.

Adults thus spent more time basking but were less grouped during the basking periods. Aggregation was thus both more and less in adults than hoppers. In all-day observations the observer had to move, and so disturb the locusts, and it is difficult to ensure that some differences were not artifacts. The wandering experiments (p. 447) suggest that undisturbed adults were inactive but disturbance could much increase their range of movement because of flight. The earliness of morning descent and spreading to exposed ground may thus be due to disturbance. Spreading out was found not to be entirely an artifact, for adults were found exposed when millet was approached for the first time during the day on several occasions. Adults move little by walking, so the scattering on open ground and return to millet in the evening

were probably in part carried out by short flights, which were observed rarely, probably because they were individual.

Such spontaneous short morning and evening flights from and to roosting places have been recorded in both "sedentary" and migratory populations (see p. 448). In migrating swarms the main flight is often begun when locusts are on the ground, having spent the night on trees etc., coming to ground by short flights and returning in the evening (Predtechensky, 1935). Zolotarevsky (1934b) records morning flights from upper slopes to valleys and return in the evening by *dissocians* *Locusta* swarms, and suspected (1936) that similar flights between bare ground and ground with grass tufts were made by solitary *Schistocerca* adults. In the latter his observation might be also interpreted as of movements in relation to high midday temperatures rather than morning and evening flights. Hussein (1937) observed *Aiolopus strepens* Latr., and *Euprepocnemius plorans* Charp., sheltering in cracks in bare ground during the night and cold days and flying to cultivated fields to feed on warmer days, returning in the evening.

Such flights are distinct from migratory flights proper made by gregarious swarms, usually at higher day temperatures, and it seems that undisturbed take-off and short flight may be a feature of diurnal behaviour even in solitaires.

The behaviour of adults spreading on bare ground outside millet should therefore be considered. After the morning ascent is completed, increase of activity continues stimulated by rising temperature, light intensity and wind strength, leading in most cases to descent by crawling but, in others, to taking off. It is not surprising that the take-off results in a descent to open ground if locusts have been roosting along the edges of the millet, as they are still sluggish and glide rather than fly. The possible attraction of heat re-radiated from ground, or thermotopotaxis (see p. 506), cannot be excluded. On the ground, some walk to sheltered positions, and the Wandering Experiments showed that they could remain inactive even on bare ground unlike hoppers. Negative thermokinesis may play a part, at least for a time, after the descent. When sun temperature on sheltered ground rose over 40° C. the locusts crawled as a result of positive thermokinesis until a windy, cooler situation was found (E figs. 10 and 35). In such positions sun temperature did not exceed 40° C. even on 27.iii. (fig. 35), but soil temperature reached 56° C. and, when it approached 55° C., adults abandoned the ground, presumably as the result of thermokinetic reaction from tarsal receptors, and visual attraction directed them back to the millet. Disturbed descents by adults in the midday period were observed on 27.iii., and on the ground the insects paused and lifted one foot after the other and finally walked or flew to the millet.

The post-meridional descent to open ground by a minority of the adults occurred like the morning one, when remaining on the ground became again possible with falling soil temperature and the weakening of positive thermokinesis.

Flights occurring in the above phases are less difficult to understand than the evening flights. Resurgence of taking off in the evening may partly be due to falling temperature, but the observations on pp. 450-453 suggest that the light conditions (relatively low intensity of unequally distributed illumination) at sunset probably played an important part. Adults in the millet made the evening ascent with the hoppers at varying times according to vegetation density, but outside the millet they remained on the ground until sunset, and flights took place under the then prevailing peculiar light con-

ditions. That locusts did not usually fly west and leave the millet may be due to interference by visual attraction to millet. There is evidence of desertion of millet by spontaneous flight in exceptional circumstances, when visual attraction to millet was evidently inadequate (see pp. 449-454) to stop it.

Mass behaviour on other zones was not observed, for adults were too few. Observations on individuals in Ia have been described (p. 445). Had adults been more numerous in the non-concentration zone, aggregation could scarcely have been appreciable, considering the low activity of adults and the relative uniformity of the micro-climatic field. Some aggregation might have been expected in the area with large bush-bearing mounds (pl. 4, fig. 7), and was to be expected in IVa, had the locusts remained there as adults.

To summarise, except for short flights by a minority, particularly in the morning and evening, which increased their range, adults were less active than older hoppers, but followed a similar daily routine. They remained longer in one place on the ground and some moved to open windy ground at midday instead of climbing the millet. Thus individuals remaining in the millet were more persistently aggregated than hoppers in the same groups, but the proportion of adults in the groups was smaller than that of hoppers. The net effect was to reduce aggregation when the adult stage was reached.

7. Discussion of aggregation.

Aggregation is defined (p. 406) as the grouping in close contact of the individual solitary locusts within the concentration areas. It is assumed to be a necessary stage, but in the past it has been taken for granted rather than described or analysed.

Two types are described above: first, temporarily aggregated conditions to which disturbed hoppers, or adults, may be subjected; second, prolonged aggregation in groups basking on the ground. The former simulates closely conditions in bands or swarms, but is so infrequent and short-lived that alone it would have little chance of leading to gregarisation. The latter is so much more permanent that while individuals are inactive most of the time it offers a better starting-point for gregarisation.

The causes of the first type are obviously external. An attempt is made in this paper to show that external factors may account for the second also. The causes of aggregation are not those of concentration, the key factors of which are the braking effect of vegetation, visual attraction to conspicuous vegetation, stimulation by wind on open ground, and the relative uniformity of the temperature field in non-concentration zones. The nature of the concentration zones prevents these factors being the key ones in aggregation; these are thought rather to lie in the patchy nature of the temperature field in the concentration zones. Thus the theoretical distinction between concentration and aggregation has a practical meaning.

Maxwell-Darling (1936) appears to have missed the stage of basking group formation by older solitary hoppers on the Sudanese coast. He described "disturbed aggregation" in young *congregans* hoppers of the 2nd winter generation (1934) which otherwise spent their time on *Heliotropium* mats, when older hoppers of this generation were already marching. The formation of basking groups is not difficult to overlook.

Solitary adults in Kordofan studied by Maxwell-Darling (1934) kept to a "sun temperature" of 38-42° C. all day, which supplies the basis of group formation in suitable conditions of vegetation and population density. Karan-

dikar's observation (1933a) on *Schistocerca* on the Pasni "reks" also showed individuals of the solitary phase exhibiting a diurnal routine, including basking, but its relation to potential aggregation was not stressed. Ramchandra Rao (1937b *et ante*) concluded that outbreaks occurred in or near millet (*Andropogon*). Behaviour was not observed where they occurred but, with Karandikar's and my observations, this conclusion involves aggregation as a stage in the outbreak process. Predtechensky (1935) records that *dissocians* and solitary hoppers of *Schistocerca* in later instars, while much less active than gregarious ones, made vertical movements during the day, descending to the ground when vertical temperature differences were marked. As at Hamashameb, the first 3 instars did not leave the plants. Zolotarevsky (1936b) also gave figures to show that diurnal movements of *Schistocerca* solitary adults could be correlated with temperature differences.

Johnston and Buxton (1937) observed that bare spaces in grasslands were "required for basking in the sun, a favourite habit of this species [*L. migratoria migratorioides*] and for egg-laying." Grasslands without such spaces were practically not inhabited by the locust. It is apparent that with a dense population, aggregation on the bare spaces would have resulted.

In *C. italicus* and *turanicus* no phases are known and dense swarms are not formed and the species seem more allied in their behaviour to the solitary than to the gregarious phase of the true locust. Zimin (1931, 1934) described how these species show a diurnal regime related to temperature, and similar to that of solitary *Schistocerca*, except that loose migrations of both hoppers and adults are an important additional feature.

True grasshoppers also include a period on the ground in their daily routine (Parker, 1930 on *Melanoplus m. mexicanus* Sauss., and *C. pellucida*; Vinokurov and Rubtsov 1930, and Rubtsov 1935, on Siberian Acridids; and Ivanov, 1934 on *Ramburiella turcomana* F.W.). Vinokurov and Rubtsov, Rubtsov and Ivanov specifically mention formation of aggregations "in habitats with open vegetation and bare well warmed patches of ground," and attributed this to external factors acting on the insects.

The occurrence of the second type of aggregation was thus expected on the basis of the known facts, although its importance for outbreaks was not emphasised.

Possibility of aggregation in vegetation zones other than millet should be mentioned. In other permanent reserves of *Schistocerca* in Baluchistan or north-west Africa, absence of unweeded millet cannot preclude the possibility of aggregation which was observed also in other zones at Hamashameb (p. 511). It is possible that on ground such as a Baluchistan rek (Karandikar, 1933b) the lee side of the tufts would form a basking-place and the total area of these is a small proportion of the whole. Photographs of places on the Mauritanian coast (French West Africa) (Zolotarevsky and Murat, 1938) reveal no conditions conducive to aggregation. In other species, in regions with totally different vegetation, aggregation may be expected in certain circumstances (Johnston and Buxton, 1937).

8. Summary.

1. Sedentary populations did not in all circumstances spend all their time on vegetation.
2. 1st-3rd instar hoppers spent most time on undergrowth in all types of vegetation. A small minority sometimes basked with older hoppers.
3. Older hoppers showed a well-defined diurnal routine, especially in zones

where wind shelter is high and continuous. In less well-covered zones it is not so clearly defined, but discernible. The routine is similar to that of gregarious hoppers except that the groups formed are not compact bands and no marching was seen.

4. Diurnal behaviour of older hoppers was studied in detail. Unlike *gregaria*, all phases of solitary behaviour may be attributed to external factors affecting each individual separately.

5. In the principal concentration zone at Hamashiameb, unweeded millet, wind and light probably played a part, but temperature and gravity seemed the chief factors. Little correlation between behaviour and humidity was found.

6. Reactions to temperature, including the important negative thermokinesis, resulted in a majority spending most of the day on small bare patches. Rough experiments confirmed negative thermokinesis in older hoppers.

7. Each individual's temperature reactions, combined with the restricted space for basking in relation to the number of hoppers in the vicinity, caused formation of groups on the patches. These persisted all day on cool days, but on hot days they broke up during the midday hours.

8. The diurnal routine of adults was similar to that of older hoppers.

9. The daily range of movement was greater in adults than hoppers, owing to their flights, and some basked near, but outside, the millet fields.

10. Apart from short disturbed or spontaneous flights adults were less active than older hoppers. A larger proportion remained on the millet all day and those basking remained longer in one place.

11. Formation of basking groups constituted a form of Aggregation. Momentarily aggregated conditions were imposed occasionally on hoppers and adults by disturbances.

C. GREGARISATION.

Observations on phases *gregaria* and *dissocians* at Hamashiameb will now be described. Differences between their behaviour and that of phase *solitaria* will then be considered and the nature of gregarisation discussed.

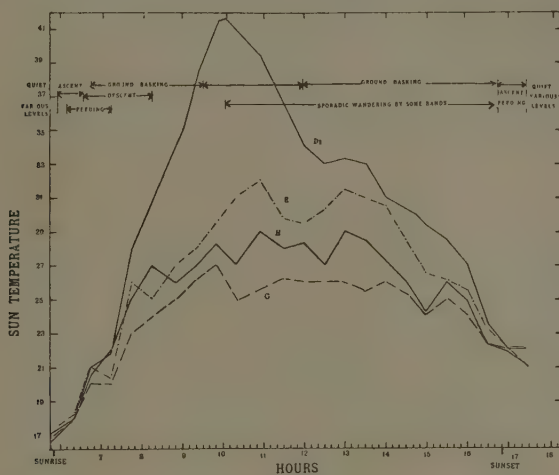
1. Daily behaviour of phases *gregaria* and *dissocians*.

Observations were made on diurnal behaviour of 1st and 2nd instar gregarious hoppers in January, on 5th instar *dissocians* hoppers in March, and on *dissocians* adults in March and April. No observations were made on large wandering hopper bands or adults in swarm formation.

(i) Young gregarious hoppers.

The observations were made in weather generally cool and cloudy. Wanderings only involved part of the hoppers and were not sustained. Hoppers thus became dispersed in vegetation and were finally poisoned. Before dispersal the young hoppers, which hatched in clean millet in "Unnamed Khor," collected on the only undergrowth, *H. undulatum* mats (pl. 3, fig. 4), on sandbanks at the edge of the millet. Observations were made on these and all-day observations on behaviour with parallel micro-climatic readings in selected positions were made on 17.i., 19.i., and 28.i. Diurnal behaviour closely resembled that of older indigenous hoppers except that basking bands were very compact, some bands wandered, and at midday the ground was abandoned at a lower temperature. The maximum number of hoppers in a band was 50, most had 10-30, some 5 or 6. On 17.i., rain fell and sun temperature

on basking-places did not reach 30°C . Hoppers descended in the morning and remained in sheltered positions in small bands all day, climbing plants again in the evening. On 19.i. maximum sun temperature was 33°C . and again there was no wandering or midday ascent. 28.i. was warmer and sun temperature on basking-places exceeded 40°C . Fig. 33 shows the sun temperature of 4 positions on this day with notes on behaviour. Fig. 34 shows to what extent available temperatures were occupied (see p. 469) by stationary hoppers. Incidental temperatures are used to supplement the data in fig. 33. Fig. 34 illustrates the precision with which hoppers keep to the warmest situa-



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FIG. 33.—“Sun temperatures” at selected positions on a *Heliotropium undulatum* “mat” (pl. 3, fig. 4) during 28.i., and outline of behaviour of young gregarious hoppers in bands.

C_2 : 15 cm. off ground alongside heads of *Heliotropium* in middle of “mat.” Wind speed at 08.30, 2.2 m./sec.

D_1 : 5 mm. off bare ground close to lee edge of the “mat.” Wind speed at 08.30, 0 m./sec.

E: 5 mm. off ground of exposed dune away from “mat.” Wind speed at 08.30, 3.0 m./sec.

H: 5 cm. off ground among stems of *Heliotropium* in middle of “mat.” Wind speed at 08.30, 0.5 m./sec.

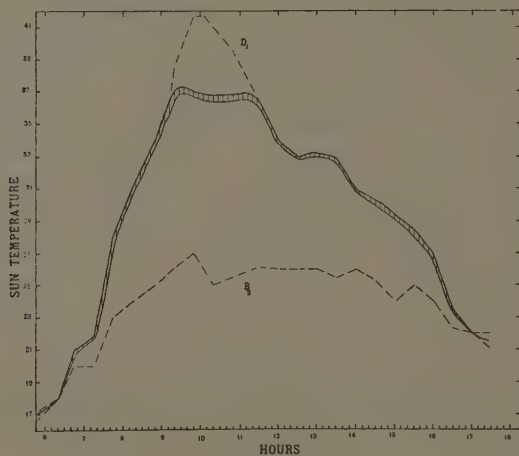
tions available, not retiring to “unnecessarily” cool ones at midday, unlike other stages and phases (figs. 12, 13, 36).

Having spent the night on *Heliotropium*, hoppers began to move at sunrise (05.50) and ascended to the tops. Part of the mat was shaded by *Suaeda* bush, but the ascent occurred there also, showing that it was not connected with the radiant heat in the positions ultimately reached. Hoppers began to feed soon and the ascent ceased in about 30 minutes. Feeding, when many hoppers crawled about and left the tops, continued for 30 minutes, but the descent had begun at 06.45. The few left at the top were now orientated perpendicular to the sun’s rays.

The descent was as described by Lépiney (1930a, 1933) in gregarious hoppers.

Hoppers began to jump, often landing on another stem, but many on the ground, whether sunlit or shaded. This continued and some landed again on plants and climbed the stems. Gradually small bands collected in sheltered sunlit spots where thermometers showed higher readings than in the shade or in the sun on top of plants. It was clear that bands formed because hoppers landing on the shaded ground did not stay there as did those coming to sunny sheltered spots where they became relatively quiescent. Those in the shade of *Suaeda* bush remained near the tops of plants, crawling and feeding but not hopping, until 07.30, *i.e.* an hour after hoppers elsewhere had been jumping and formed basking groups. After that hoppers in the shade disappeared, presumably coming down.

From then until 09.30, and from 11.30 until the evening ascent at 16.45,



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FIG. 34.—Distribution of non-wandering gregarious hoppers in relation to the range of available "sun temperatures" on 28.i.; based on fig. 33 and other readings. For further explanation see fig. 12.

basking bands were all over the *Heliotropium* mat and in the grass tufts. Fig. 34 shows that they were occupying the warmest available situations, and, judging from cigarette-smoke trails, also the best sheltered positions.

In millet the basking primary bands of new-hatched gregarious hoppers showed outlines coinciding with those of shadows cast by leaves. Most were fairly quiet but those which moved and came to the boundary of sun and shadow turned away, in few cases without completely entering the shadow. This apparently phototactic behaviour was not observed in basking solitaires. It may be latent in solitaires, but considering their lower activity level, it was not unexpected that phototaxis may be of less importance in causing their basking. This reaction, unless very strong, requires frequent encounters with the "boundary" before becoming of critical importance.

When hoppers became temporarily shaded by leaves moved by wind they did not move, but if shaded for a minute or so they hopped and scrambled

to the main band in the sun. This recalls the activating effect of shading on solitaries quoted as evidence of negative thermokinesis.

All the warmest positions available were not occupied by hoppers. Small bands were situated within a few centimetres of each other, and often neither thermometers nor smoke trails revealed appreciable difference between situations occupied or vacant. Simultaneous measurements of temperature and air movement, comparing places from which bands were driven and those within a few centimetres where no hoppers had been, were made about 20 times. Appreciable differences were shown between depressions 1–2 cm. deep and the open sand, or the lee and windward sides of tiny grass tufts, in which the warmer and better-sheltered position was occupied. As long as there was no difference in air movement, cases were repeatedly found when a thermometer in a place where no hoppers had been read the same as, or 1° higher than, a place from which a band had been driven. This indicated, first, the importance of the thermal or mechanical effect of air movement, and, an additional factor, that gregarious inter-attraction was required to explain the distribution of hoppers in compact bands.

In the morning hoppers in the stationary bands became more restless and by 09.30 those in the warmest places might be described as gently "seething." At a given moment at least one-third were jostling and sometimes scrambling over their fellows. Bands in less sheltered positions were quieter. After 09.30 seething increased and bands moved *en masse* from ground to the bases of *Heliotropium* stands, seldom climbing higher than 2–3 cm. Sun temperature in some places on the ground rose to 38–42° C., but where hoppers were clustered remained at 35–39° C. On 28.i. the hottest time was not at midday but at 10.00, and at 12.00 stationary hoppers returned to the ground where temperature was now about 34° C. At 16.45, just before sunset, hoppers began to climb or jumped to the stems whether the ground was sunlit or not. Most hoppers became shaded before the ascent began, but thermometers read higher on the ground than on the tops of the plants and many hoppers did not have time to reach positions exposed to the last rays of the sun. The ascent merged into general creeping and feeding till movement died down and ceased 40 minutes after sunset.

Although stationary bands could be found throughout the day, sporadic wanderings occurred from 10.00 until sunset. Close observation of the wandering was made as the bands were small and wandering incipient.

In certain circumstances, notably changes of radiation intensity, excitement showed a sharp increase and some hoppers jumped so far as to leave the band. A few followed, each stimulated to a further jump by that of another past it. Usually the vanguard settled into quiescence in a new well-sheltered sunny position in grass etc., before all the hoppers had left the previous basking-place. The effect was a slow advance through the undergrowth as hoppers were gradually drained off one basking-place into the next, advancing bands losing considerable numbers in the process.

Often wandering began with no apparent stimulus and was obviously sustained by mutual stimulation. A sudden increase in solar radiation often preceded the emission of a "volley" of jumping hoppers from a stationary band, but on numerous occasions sudden decreases in radiation also caused hopping to start. No wandering was observed until 10.30, when the sun went in more suddenly and completely than all morning and, a minute or two after, "volleys" of hoppers were seen leaving all bands. On 26.i., bands were observed all day over a large area and no "volleys" or wandering was seen until 40 minutes

before sunset. A minute or two earlier the sun suddenly disappeared behind a dense cloud. Hoppers began to jump away from a *Heliotropium* mat and wandered until shortly after sunset, when they became scattered and began to climb and feed. Ground temperature fell from 23° C. to 22° C. when the sun went in. On neither occasion was a sudden change in wind strength or other observable factor noticed to coincide with outburst of marching.

This appears to indicate that gregarious as well as solitary hoppers were sometimes activated by decreases in intensity of radiation. The time relations are consistent with experiments on indigenous hoppers (p. 500). On two occasions behaviour of bands of 30–40 hoppers was observed for over an hour with minute to minute readings of a black-bulb thermometer. In the first case, when the black bulb fluctuated between 34° and 37° half the time, and 27° and 31° for the remainder, activity varied much, decreasing after a temperature rise in 7 cases and increasing after a temperature fall in 17, this being in harmony with the hypothesis of negative thermokinesis, but also decreasing after a fall in 10 cases and increasing after a rise in 6. The results are therefore inconclusive. In the second case temperatures were higher, between 35° and 42° in the black bulb, and temperature rises always produced increased activity. Dominant positive thermokinesis at such temperatures was to be expected.

Outbursts of marching among gregarious bands are not recorded as associated with decreases of radiation; on the contrary, when such are mentioned their effect has been to stop marching bands (Uvarov, 1921; Sviridenko, 1924; Zimin, 1934; Fraenkel, 1932). The contradiction may be due to the larger size of bands observed by these authors. In a large marching band the initial outburst after a temperature rise (figs. 28–30) would be maintained by mutual stimulation so as to destroy any latent negative thermokinesis.

The possibility of negative thermokinesis has generally received little attention. I have suggested the inactivising effect of higher body temperature as the cause of quiescence on sunny positions on the ground, ending the random movements of the morning descent. The random nature of the morning descent is stressed by Lépiney (1930a, 1933), thus strengthening evidence against thermotopotaxis. If marching always immediately followed descent mutual stimulation and attraction would account for the latter, but instead basking bands are formed. Lépiney also admits the possibility of immobilisation by irradiation in the formation of morning basking bands but somewhat slurs over the probable distinction between orientation reaction and negative thermokinesis. Thus his interpretation approaches mine and he is no less emphatic that the descent is unconnected with "thermotropism." Descent, however, consists not merely in some hoppers reaching the ground (as he records, many re-ascend), but is the result of a dual process of random vertical movement and of negative thermokinesis, the combined end-effect of which is a descent. Unless Lépiney's "thermotropism" is restricted in meaning (to thermotopotaxis), temperature, and so thermotropism is concerned in the descent as well as in the distribution of the bands formed (see Appendix 3).

(ii) *Older dissocians hoppers and dissocians adults.*

Some of the gregarious hoppers which hatched in clean millet in the mouth of Khor Toqwan remained to become adult at the end of March. They were left when the main body marched away, preserved their band formation and wandered in the millet, but in the 5th instar, when they were studied, they

had lost some of the black pattern on their bodies. This was a clear case of loss, or non-development, of pigment associated with lack of intensive gregarious activity, due in turn to the density of vegetation. At the same time, gold-green coloured individuals, not in bands, and almost solitary in behaviour, were present in Khor Toqwan, particularly at the north and south ends of cultivation where vegetation was densest. These were more active, easily disturbed and more alert than the solitaires. The rapidity and precision with which they moved round a stem or leaf, keeping the stem between them and the observer, was striking. Such excitability was noted by Johnston and Maxwell-Darling (1931) in solitarily living *dissocians* *Locusta*. No young solitary hoppers existed at Hamashameb to produce these older hoppers, and they were extreme *dissocians*, as the average E/F ratio (over 2.1) of ensuing adults showed. They had not been in band formation since 1st or 2nd instar and their solitary life left them without black pigmentation in the 5th instar. Johnston (1934) described a similar case where an original band split in two, one entering short grass (*Cynodon*), to become sedentary and solitary, the other moving to the bush, to remain active and gregarious.

The behaviour of both types and of recently moulted adults derived from the more gregarious hoppers was observed throughout 27.iii., with parallel readings of temperatures. Behaviour of extreme *dissocians* hoppers resembled that of indigenous hoppers and is referred to above (p. 511). Behaviour of adults was also indistinguishable from that of indigenous adults despite their being derived from hoppers in band formation. This further emphasised the scattering tendency of adults. Behaviour of the black-marked near-gregarious *dissocians* hoppers was intermediate. It resembled that of young gregarious hoppers in dull weather: that is, wandering was loose and inconsistent.

Sun temperature in several positions on 27.iii. is shown in fig. 35, with outlines of behaviour of three types present. Morning ascents and beginning of the descents occurred simultaneously. Green hoppers required longer to descend than black hoppers or adults. Most black hoppers came to the ground, but an appreciable minority of the green ones and a larger minority of adults were on millet throughout the day. Basking of adults and green hoppers on the ground in the millet continued until 09.20, when sun temperature on the ground was about 42° C. Green hoppers then climbed the millet and stopped at lower levels in the sun. Most adults also climbed, but some continued to spread on open ground outside the millet (e.g. position E₁) or even to unsheltered places (E). Black hoppers, however, had left the ground at 08.50, when sun temperature on sheltered ground in millet was only 39° C. On the millet stands they clustered at medium levels in sun, or lower levels in shade, thus keeping in cooler positions than green hoppers. While most black hoppers were in bands, some were scattered, and these also left the ground earlier, when the green hoppers were still basking. Thus each black one, apart from mutual stimulation, was reacting to temperature differently from the green hoppers.

As temperature rose, around 11.00, the black hoppers climbed to the top of millet or moved to the shade at medium levels; green ones also climbed further, but remained in the sun at medium levels or in shade at lower levels. Adults mostly climbed to the top and those outside the millet (now only in the windiest positions) abandoned the ground and walked or flew to the millet. When temperature again fell after midday all types began to descend slowly, adults re-appearing on the open ground at about 14.00. Green hoppers resumed basking at 15.15. Many black hoppers did not again descend that day, but here and there bands left the millet and hopped to the ground as early as 13.20,

where temperature was 50° C. They wandered about in loose bands in the millet. As temperature fell, wandering decreased and bands became stationary in the sun about 16.00, 45 minutes after green hoppers had resumed quiescent ground basking. The commencement of the evening ascent varied according to the time when ground became shaded. Green hoppers, black ones on the millet, and adults in it, ascended at about the same time, wandering black ones somewhat later, and some adults outside did not return until nearly sunset.

The respective relations of the three types to the available temperatures are shown in fig. 36, where allowance is made for E and E_1 in fig. 35 being available to adults but not hoppers. Fig. 36 shows that black hoppers could not remain quiescent on the ground at temperatures at which green *dissocians* and *solitaria* hoppers could. The black ones climbed or wandered while the green ones were still basking. Plain thermometers not being influenced by radiation as the bodies of insects are, relations of behaviour to a given thermometer reading are

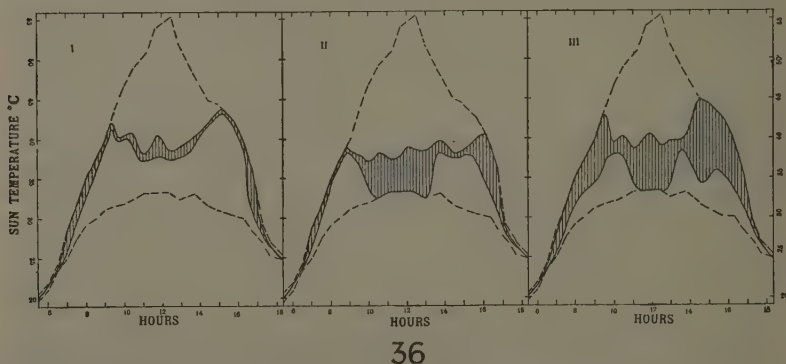
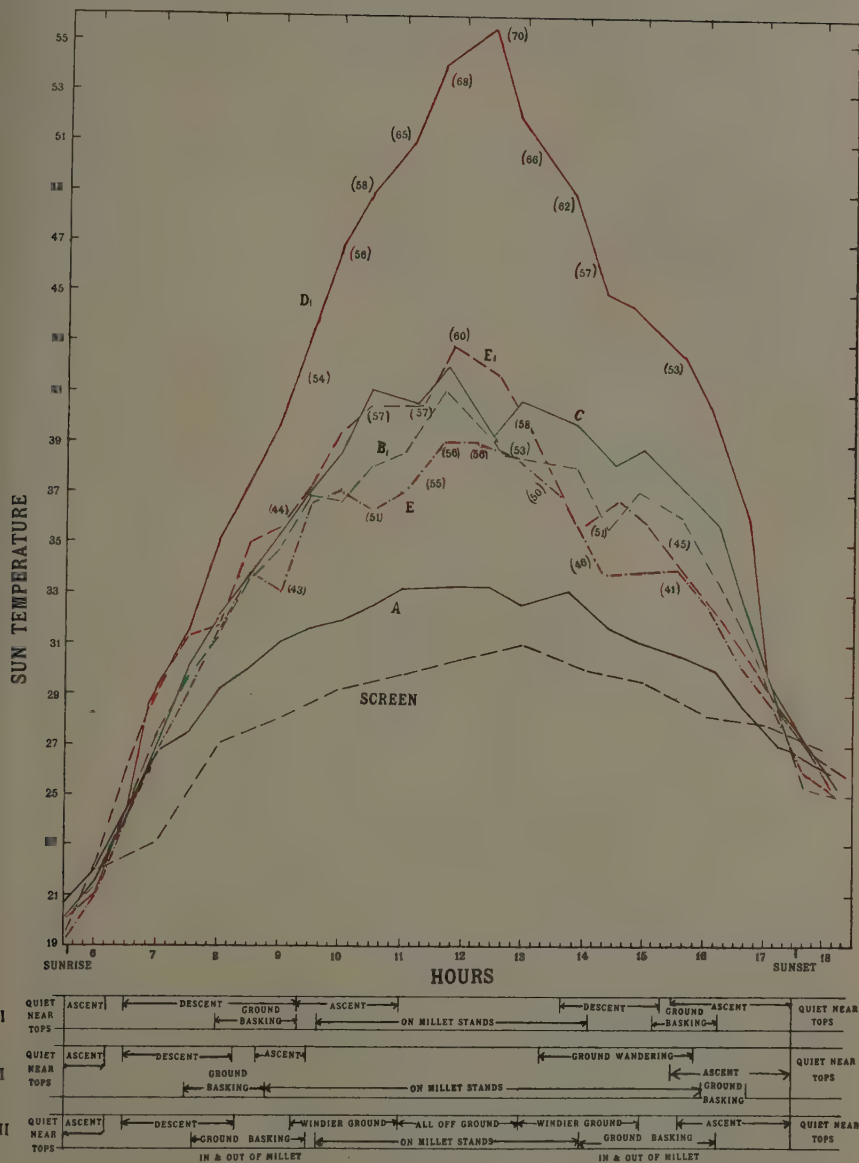


FIG. 36.—Distribution of I. green solitary-living *dissocians* hoppers, II. near-*gregaria dissocians* hoppers in bands, and III. solitaria-living *dissocians* adults, in relation to the range of available "sun temperatures"; based on fig. 35. For further explanation see fig. 12.

not comparable on different days, but on 27.iii. the different relations of behaviour of near-*gregaria* and near-*solitaria* to the time of day proves, regardless of thermometers, that quiet basking is prevented by lower temperatures in the former than the latter. This seems due to one (in isolated black hoppers) and probably both (in black hoppers in bands) of the following factors:—first, higher body temperature of black hoppers under radiation (Hill and Taylor, 1933; Strelnikov, 1936a) which raises the level of the curve of activity in relation to external temperature; and second, the mutual stimulation to which gregarious hoppers in bands are subjected and which would have the same effect. Thus the relation of external temperature and activity of pigmented hoppers in bands may be expressed schematically by the broken line in fig. 31.

The groups of green *dissocians* hoppers in clean millet were loose, like indigenous hopper groups, and seldom included more than 5 individuals. Many basked singly and many remained on the millet, and that groups were formed at all was probably due to local air currents rather than gregariousness (see



"Sun temperatures" at selected representative positions in millet without weeds (pl. 5, fig. 9 and pl. 6, fig. 11) during 27.iii., and outline of behaviour of the majority of I. solitarily-living green *dissocians* 5th instar hoppers, II. near-gregarious *dissocians* 5th instar hoppers in bands, and III. solitarily-living *dissocians* adults. Figures in brackets are the soil surface temperatures at the positions and times shown.

A: 1.5 m. off ground among millet heads (pl. 6, fig. 11).

B₁: 90 cm. off ground lee side of clearing among millet.

C: 15 cm. off ground lee side of clearing among millet.

D₁: 5 mm. off ground lee side of clearing among millet.

E: 5 mm. off ground on bare exposed dune outside millet.

E₁: 5 mm. off ground lee side of bare mound outside but close to millet.

p. 485). Indigenous hoppers were never so numerous in clean millet as the *dissocians* hoppers and their behaviour was not studied, so that a direct comparison is impossible. The scattered distribution of basking individuals may therefore have had nothing to do with real differences in behaviour of *solitaria* and *dissocians*.

However, similar green *dissocians* were also present in the dense irregular vegetation forming the northern edge of cultivation in Khor Toqwan (pl. 6, fig. 12) and in similar numbers to their indigenous predecessors there. No all-day observations were made on these but the place was visited frequently, and basking groups were not formed as they were by indigenous hoppers. While some basking and group formation probably occurred basking was significantly less in *dissocians* hoppers than the similarly coloured indigenous ones. Perhaps the reason is that *dissocians* loses the black pigmentation characteristic of phase *gregaria* earlier than the high metabolic rate and excitability, also characteristic of it. If so, the lack of group formation in green *dissocians* hoppers could be explained as follows. When hoppers gathered on a basking-place by their reactions to external factors, extra excitability (see p. 521) would tend to exaggerate the mutual stimulation evident even in basking groups of indigenous hoppers (p. 465). They would start to move, just as black hoppers on 27.iii. went on moving when basking-place temperatures permitted quiescence of green hoppers (figs. 35, 36). In millet with weeds movement would immediately carry them off the basking-place into the undergrowth and destroy the group. This amounts to a suggestion that in fig. 31, a curve for *dissocians* hoppers with as little black as solitary hoppers, would lie not along the curve of the latter, but between it and that for gregarious hoppers (see below, p. 524).

Another interesting observation concerned with comparative behaviour of *solitaria* and *gregaria*, was the presence of indigenous hoppers among marching bands. At the end of February long columns of young hoppers marching southwards, both in- and outside the cultivation, made their way along lanes of bare ground in the undergrowth. Some green indigenous 3rd-5th instar hoppers were seen in the bands, sometimes being carried out of the cultivation. Close observation showed that indigenous hoppers were not carried more than 5-6 metres and their marching differed from that of gregarious ones surrounding them. The latter hopped in regular jumps interspersed with crawling, the jumps apparently stimulated by another hopper catching or overtaking them. The indigenous ones were more irregular in movement; they appeared also to be stimulated by others, but after a few jumps stopped movement for some seconds and then jumped vigorously again. Their movements were not so uniform in strength, or so equally spaced in time, as those of the gregarious ones. Eventually each solitary hopper left the main stream and the band by a series of vigorous jumps, and entered near-by vegetation.

Several authors have made similar observations (Uvarov, 1921; Johnston, 1926; Strelnikov, 1936a; Zolotarevsky and Lépiney, 1934). Zolotarevsky (1929) described solitary hoppers of *L. m. capito* in Madagascar forming a fringe, jumping irregularly in front of the bands and stopping as they got clear.

This suggests the existence in solitary hoppers of a latent capacity to respond by forward movement to images of other hoppers moving past. This exists in a crude, unreliable form not sharply distinguished from the ordinary response of solitary or gregarious hoppers to disturbances in the visual field and is too weak to keep hoppers in the advancing bands for long. Incapacity of solitary hoppers to maintain the steady high activity demanded of the marching bands is also suggested by the observations.

2. Discussion of the nature of gregariousness.

Behaviour of *gregaria* individuals differs from that of *solitaria* in several points. One concerns the higher metabolic rate and excitability of individual gregarious hoppers apart from the effects of life in a band (see above). Butler and Innes (1936) established that gregarious *Locusta* have a higher metabolic rate (per unit of surface area) than solitaries even when inactive in the laboratory. In the field body temperature of gregarious hoppers influenced by solar radiation, is higher than in solitaries (Buxton, 1924; Hill and Taylor, 1933; Strel'nikov, 1936a), and Uvarov (1928, 1937) deduced that the activity of gregarious individuals must be higher than solitaries under the same conditions (fig. 31). Behaviour of black hoppers at Hamashiameb on 27.iii. confirmed this (fig. 36). Strel'nikov (1936a) suggested lower specific gravity as another factor facilitating greater activity of gregarious individuals.

Apart from the above differences, apparent in gregarious individuals in the absence of their fellows, there are two kinds of difference associated with life in bands or swarms.

The first simply adds to the greater activity of individuals by mutual stimulation, which no doubt takes place. It is most strikingly shown where a flying swarm "picks up" a resting swarm from the ground (Johnston and Maxwell-Darling, 1931), and Sviridenko (1924) recorded that dung-beetles flying past adults of *Doclostaurus* cause the latter to fly up and follow.

There has been some discussion as to the nature of mutual stimulation. Uvarov (1928) quotes Vayssi  re (1921), who considered air vibration, of a type which locusts discriminate from that caused by thrown stones, as the agency by which a locust stimulates another to take off when flying over it. Uvarov was inclined to agree, adding: "There can scarcely be any doubt that the same reflex may be due to visual stimuli, but these are of secondary importance, since L  pincy (1928) found that blinded locusts respond to the approach [of a man], while normal ones put behind a glass do not." L  pincy has since (1930c) got results contradicting this. Blinded locusts did not fly on man's approach, on being thrown into the air, or when the mass take-off of their fellows occurred; two days later they behaved in the same way. Uvarov (*loc. cit.*) stated that visual disturbances can cause jumping without air or ground vibration reaching the insects. It was often noted at Hamashiameb that hoppers, in bands or solitary, were not disturbed by an observer while they were still, but a sudden movement of his head or arm would cause immediate jumping (see also Johnston and Maxwell-Darling, 1931).

La Baume (*in* B  cher, 1918) wrote "Vor allen Sinnen der Heuschrecken ist offenbar der Gesichtssinn am sch  rfsten ausgebildet." The sharply demarcated "front" noted by many authors (Uvarov, 1928, fig. 46; Fraenkel, 1932; L  pincy, 1933) which is formed by the foremost hoppers of a marching band on open ground confirms the visual nature of mutual stimulation. Such front, with no hoppers beyond but many along it, thinning out to a ragged rear, is inexplicable by mutual stimulation by air or ground vibration, but is understandable if one supposes that the forward movement is stimulated by sight of an adjoining hopper catching up.

For these reasons it is no longer justifiable to ascribe to air vibration the primary r  le in mutual stimulation, and visual images must be regarded as more important.

The second difference in behaviour of *gregaria* and *solitaria* associated with life in bands and swarms is the evident interaction between gregarious individuals and their tendency to move together and in the same direction. While physio-

logically these may be interconnected with mutual activation they are separable, at least in effect.

Uvarov (1928) and Fraenkel (1929) speak of an "instinct of imitation." Lépiney (1933) remarks that imitation is a needlessly complicated conception applied to the interaction of gregarious individuals. I suggest that the term "imitation" in part merely expresses the raising of the general activity level by mutual excitation. For the rest it expresses the fact that movements produced are clearly related between one individual and another.

The second fact, of keeping together members of a band, evident both in basking and marching bands, is described by Uvarov and Fraenkel as a separate instinct ("Aggregation"). Observations of Fraenkel (1932), Lépiney (1933) and at Hamashameb show that the distribution of quiet basking bands cannot be due only to the horizontal temperature field. Some inter-attraction is at work, the necessity for which is more clear when cohesion of marching bands and flying swarms is considered.

Despite Lépiney's (1933 *et ante*) evidence that olfactory "chemotropic" responses are concerned in inter-attraction, field observations point definitely to visual reactions. In a marching band in open, windy country, locusts only receive the smell of their upwind fellows and those on the windward side have no reason to remain in the band, so that the band would gradually scatter to windward. In fixed basking bands, smell cannot be excluded but would only operate downwind in the slightest draught, and if visual inter-attraction exists it must operate in both cases.

Visual reactions of gregarious hoppers to each other were not investigated in the laboratory. Uvarov (1921, 1928) suggested they were an instance of "compensation" movements, a widespread phenomenon in animals, and in which each moves so as to tend (not always with success) to oppose and nullify the movement of visual images across the retina. If it be allowed that gregarious behaviour depends on visual reactions, the evidence for Uvarov's suggestion is now stronger than ever.

The facing upstream and maintenance of position in relation to the bank by fish and insects (Lyon, 1904, 1905, 1909; Schulz, 1931; Gaffron, 1934), the optomotor response of animals on turntables or stationary in revolving drums (Radl, 1903; Loeb, 1918 and others), the pursuit of moving objects (Baldus, 1926; Wigglesworth and Gillett, 1934), and even the maintenance of position in relation to the bank and band formation by Gyrinid beetles (Brown and Hatch, 1929) in which movement of individuals may be most irregular, all appear attributable to some such underlying mechanism. "Schooling" behaviour in certain fish, similar to gregarious locust behaviour, and involving stationary group formation and parallel movement in groups, is shown by Loeb (1918), Spooner (1931) and others to depend on visual reactions. Sometimes compensatory reactions are best developed in the form of anterior "fixation," whereby movement taking the image of the object away from an anterior position in the eyes is compensated, resulting in direct pursuit of moving objects, but in the case of fish or swimming insects, not merely such movements but those in any part of, and in either direction on, the retina, appear to be compensated.

This last would explain the behaviour of individuals in relation to stationary and marching bands, assuming a tendency in gregarious locusts to compensate for the movement of the images of their fellows, despite the observation that the movements are centripetal in relation to stationary, and parallel in marching, bands.

For a hopper outside, but in sight of, a stationary band the principal movement over its eyes will be caused by its own movements; if it deviates to one side, say to the left of the band, the movements from in front backwards across its right eye will stimulate it to turn to the right and so return the image of the stationary band to its original position. In effect the only way a moving individual can prevent the image of a stationary object moving across its eyes is by going straight to that object. Thus if it keeps moving it is bound to join the stationary band eventually.

When a hopper is in a band, the overwhelming majority of the movements of images over its eyes will result from movements of its fellows, in comparison with which, its own movements will contribute little. Thus, when hoppers start moving actively, the image of others across an individual's eye will cause it to turn and follow. When, in consequence, many hoppers begin moving, the image of others passing at the side will cause each hopper to continue moving forward and parallel with its fellows, thus compensating their movements.

It is thus possible to regard the "gregarious instinct" as comprising not two parts, an Aggregation and an Imitation "Instinct" (Uvarov, Fraenkel) but as a single "compensatory" reaction.

There is no good reason to suppose it is an instinct at all, since an instinct is by customary definition an *inherited* behaviour pattern. Faure's theory (1932) was that the "hyper-metabolism" of ph. *gregaria* was carried over from one generation to the next by cytoplasmic inheritance of the substance he called "locustine" (see p. 527). Assuming that all aspects of "gregariousness," characters easily acquired and lost, could only be inherited cytoplasmically, one can hardly conceive that the acquired discrimination of the compensatory reaction is inherited. The evidence suggests that, while *solitaria* and *gregaria* both inherit a latent attraction to objects and compensation reaction, the peculiar feature inherited by *gregaria* is only excitability. Thus, the added excitability coupled with the latent compensation reaction, is enough to produce gregarious behaviour in a crowd, with very little "habituation."

Vinokurov and Rubtzov (1930) on the basis of their work on Siberian Acridids considered that the behaviour of the so-called "swarming" and "non-swarming" species must be explained by the action of external, meteorological factors alone. This led them to regard outbreaks as unconnected with qualitative behaviour change. There seems, however, to be adequate contrary evidence in the case of the true swarming locusts. It is true, as they remark, that the "gregarious instinct" will not explain the movement of separate bands in the same direction, but an explanation of that would not explain why they remain bands and do not scatter. Nor is the fact that hoppers are not more active in the presence of vegetation shaken by the wind, than in that of their fellows, an argument against gregarious interaction and mutual stimulation, for it denies the hoppers all powers of discrimination, which they certainly have.

Similarly Micheltore (1934) suggested that "the behaviour of an individual locust does not depend on its phase, but on its environment, particularly the degree of crowding to which it is subjected." The inherent capacity to migrate, whatever the phase, is strongly suspected (see p. 458) but this cannot obscure the qualitative difference between the migratory tendencies of the two phases, demonstrated most clearly by the behaviour of solitaries in gregarious bands (p. 523).

Again, Uvarov (*in* Hussein, 1937) wrote: "His [Hussein's] observations show that . . . mass movements of hoppers and flights of adults which are so characteristic of locusts, are not normal movements, but are caused by excessive

temperatures. These movements are definitely due to external factors and they continue only as long as the conditions remain unfavourable. This conclusion gives a clue to the understanding of the causes of locust migration on a sound scientific basis." This is not supported by field evidence. Firstly, while high midday temperature increases the activity of solitaries it does so only momentarily, for, grouped or not, they retire immediately to cooler situations where they are no longer excited (see p. 465). Secondly, gregarious hoppers may make mass movements when temperature is not "unfavourable" but mild (see p. 520). The fundamental difference is in the mutual activation between fellow members of a band and incapacity to escape the stimuli of their fellows owing to mutual attraction. The so-called "abnormality" of the movements of gregarious locusts is therefore not primarily a matter of "unfavourable" conditions.

In conclusion it is suggested that gregarious locusts in bands behave differently from solitaries for the following three main reasons.

1. Each *gregaria* individual has a higher metabolic rate and is more excitable and active. This is enhanced by the extra heat their blackened bodies absorb from the sun and their lower specific gravity.

2. The activity is further increased by their crowded mode of life where external stimulus is magnified by mutual visual disturbance.

3. Each possesses a well-developed, discriminatory visual "compensation" reaction to its fellows, enabling bands to preserve their formation in rest or movement. This constitutes the "gregarious instinct" proper.

3. Conclusions : Gregarisation.

As no outbreak occurred at Hamashiameb in 1937, the bearing on gregarisation of the observations made could not be observed in practice, but it is possible to consider what is required for it to occur and how such circumstances might have been realised at Hamashiameb.

Faure (1932) and others demonstrated that crowding solitary individuals will cause the deposition of black pigment characteristic of *gregaria*. This is attributed to "the excessively high rate of metabolism obtaining in swarm life" which, by producing "locustine," leads to black coloration, and further increases activity. Thus while numbers and external conditions remain the same, there is no escape from the vicious circle which produces gregariousness (Faure, *loc. cit.*). Husain and Mathur have established conclusively (1936) that this coloration can be produced by forcing activity in isolated solitaries.

This led Uvarov (1937) to conclude "increased activity is the primary stimulus to the transformation into the gregarious phase." The behaviour of *gregaria* is, however, not explicable only on the basis of greater activity, and experiments quoted provide only a basis for understanding the colour change and its presumed consequence, increased activity. Experiments where the coloration is produced by forcing activity would only solve the problem of phase change if the "gregarised" individuals produced were not only more active but more capable of behaving in a gregarious manner instead of hopping irregularly when placed in bands of gregarious individuals. Unfortunately this has not been tested.

In the field, externally increased activity has only been suggested in one case, the "driving" of *Locusta* hoppers before rising flood water (Lean, 1936). At Hamashiameb there was no evidence that this factor varied annually or contributed to gregarisation. On the contrary, before increased activity was

noticed, individuals were already in groups where the effect of external activating stimuli already entrained activation of one individual by another. Moreover, most of the time, those in the groups were markedly inactive. If "increased activity" refers to its increase in isolated individuals by external agencies, these individuals only subsequently and consequently developing gregarious behaviour, then it is clear increased activity in this sense need not be "primary."

"Gregarious instinct" has been suggested as a form of visual "compensation" reaction well developed in gregarious individuals in relation to their fellows, and apparent in crude form in solitaries. Uvarov (1934, 1937) suggested the development of the gregarious instinct as a case of conditioning, the instinct being the fully formed conditioned reflex. A conditioned reflex (Pavlov, 1927) is one in which an "unconditioned" stimulus, producing a given response, may be substituted by an entirely new ("conditioning") stimulus. The latter is able to elicit the said response only through repeated application either before, or coincident with, the unconditioned stimulus. The sight of fellow hoppers, assumed to be the conditioning stimulus in development of gregariousness, is not so far from other visual stimuli to which solitaries respond that the associative mechanism of a conditioned reflex needs invocation. I suggest a process of "attunement" or "habituation" in which an already existing reaction is refined and concentrated on a particular type of stimulus (fellow individuals), and by repetition discriminated from other stimuli, would fit the facts as well.

Solitaries are visually attracted to conspicuous objects (p. 431). This appears distinct from phototactic responses and more comparable to a compensation or fixation reaction. They are attracted to vegetation even when it is agitated by wind, yet are repelled by movement of other types of objects such as one's arm. It is too much to suggest that such power of discrimination is inherited. It is simplest to suggest they are accustomed to the movement of vegetation but not of men's arms, and if the latter were as constant a feature of their environment as vegetation, they would be no less attracted, not as a result of conditioning in the strict sense of association, but as a result of simple discrimination between accustomed and unaccustomed objects (Brown and Hatch suggest this in position-maintenance by swarms of Gyrinids, 1929). This derives support from the observation that solitaries may move with a gregarious band to a limited extent.

I deal now with the process of gregarisation as it may occur in an outbreak centre like Hamashiameb.

The quiescence of basking individuals appeared at first to throw doubt on the value of this type of aggregation as a step to gregarisation. Further consideration, however, led to the conclusion that formation of quiescent groups is an essential stage if gregarisation is to occur.

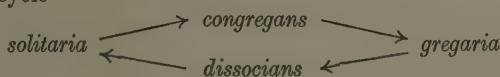
The groups are formed and maintained by external factors acting on each individual but, since groups persist most of the day, hoppers sitting and moving near by bulk larger and larger in each other's visual environment, in proportion to population density. Even before the hoppers increase each other's activity the "gregarious instinct" has a chance to develop. From the outset of group formation hoppers are forced to move simultaneously at least for a few minutes, as when disturbed, or by shading or high midday temperature. Presumably at these times fellow hoppers become especially important in the visual environment of each individual. Here it is interesting to recall first that visual attraction to conspicuous objects was especially evident in slightly excited

hoppers (p. 432), and second that Hussein (1937) found a gregarious tendency in otherwise solitarily behaving individuals when at the stage of "slight excitement" in temperature cabinets.

In the earlier months when weather is cloudy and cool, and disturbances due to men or cattle are few, quiescent group basking is general and prolonged. When hoppers are forced to move the undergrowth separates them at once, and cuts short mutual impressions and activation; this was the case with the 1st winter generation at Hamashiameb. On grounds given above, any development of the "gregarious instinct" carried out by this generation, other than raising of the metabolic rate, is not expected to pass on to the next. When a 2nd generation is produced conditions undergo important changes. Population density, and size of groups, are greatly increased and mutual activation correspondingly so. Temperature is generally higher and high midday temperature, causing movement when the groups break up, is common. Disturbance from men and cattle becomes frequent. In many places undergrowth withers and the greenest, densest vegetation is often millet on soft sand with few weeds. A greater proportion of hoppers of this generation will be on *Heliotropium* mats in, and adjoining, the millet.

As a result the new generation is much more crowded. Quiescent basking of older hoppers and adults will occur, but disturbances will cause more frequent simultaneous movements of all stages which begin to deserve the name of "mass" movements. Mutual stimulation is intensified and mass movements will tend to last longer when initiated by external agency. This is doubly true for hoppers because of the lesser proportion of undergrowth available to stop movement and separate individuals. Larger bare patches (pl. 8, fig. 16) and other bare ground in millet, or round *Heliotropium* mats outside it, assume the character of parade grounds, where hoppers receive training in mass behaviour, and mutual compensation reactions, when they are still unable to break away from thick vegetation entirely and to sustain long marches together, and would, if driven away from the millet, disperse and become solitary again. Eventually, having developed the "gregarious instinct" to a point that will prevent scattering, and raised their activity to a high pitch, locusts will leave cultivation as marching bands or flying swarms, visual attraction to the millet being overridden by mutual visual attraction and stimulation.

Gregarious bands marching through cultivation at Hamashiameb, lost an appreciable number of their members, which entered dense undergrowth, lost sight of their fellows, remained isolated and became, eventually, *dissocians*. Vegetation zones including dense undergrowth were thus inimical to the preservation of gregarious behaviour and appearance. It seemed also that *dissocians* hoppers retained a higher level of excitability long after ceasing to live in bands and were unable to form aggregations and pass back into phase *gregaria*, as easily as solitary hoppers could do. In relation to dense vegetation, therefore, the cycle



is a vicious circle. Such habitats assist solitaries to meet and become gregarious but prevent gregarious locusts from meeting and force them to become solitary.

It is now clear why a stage of quiescent aggregation is essential in the outbreak process. If increased activity appeared in the early stages when groups

are small and undergrowth luxuriant, hoppers would see little of each other. Groups would be driven to the undergrowth by only moderate temperature and mutual stimulation, and much time would be spent isolated, and the gregarious instinct have little chance to develop. The vicious circle would be complete, in modified form, with no outbreak occurring. That outbreaks do occur, is further evidence that changes in activity level associated with phase transformation lag behind changes in strength of the gregarious instinct proper, as activity and biometrical change lag behind colour change. Thus, while curves for *congregans* and *dissocians* in fig. 31 would both fall between those for *solitaria* and *gregaria*, the two former would not be coincident, but *congregans* nearer the *solitaria* curve and *dissocians* nearer the *gregaria* curve.

Doubtless the vicious circle is often completed in nature without an outbreak, especially if numbers fall too soon. Since, however, locusts are inactive enough to keep together in basking groups for a long time and re-form groups under the influence of external factors as soon as disturbances pass, the gregarious instinct is able to develop first. Then, with favourable conditions, the raising of activity to full *gregaria* level gives the impetus to enable sustained movement to carry locusts out of the outbreak centre and saves them, at least temporarily, from the return round of the vicious circle.

The act of "breaking-out" of the environment which engenders gregariousness is essential for the preservation of it, but the longer this act, and the "hyper-metabolic" state it represents, can be deferred without numbers decreasing, the more firmly established is the "gregarious instinct" which alone ensures the cohesion of bands and swarms in the vast tracts of barren country included in the invasion areas of *Schistocerca*.

4. Suggestions for prevention of gregarisation.

On the basis of my observations, some suggestions may be advanced for permanent control measures in outbreak centres similar to Hamashameb.

Outbreaks might be prevented by the elimination of concentration zones, but the following would be both simpler and more sure. All undergrowth should be removed from most of the cultivation or other types of concentration zones. Patches 4-5 m. in diameter should be left with thick uneven undergrowth and containing 4 or 5 patches of bare ground 40-50 cm. in diameter. Not more than 100 m. should intervene between one unweeded patch and the next. The patches should trap the bulk of hoppers. Poison bait should be spread in the patches once or twice in the season. Strips of undergrowth, bordering and penetrating the cultivation, might serve as well as patches.

The dimensions and frequency of poisoning are tentative; the best arrangement would be found by trial and error. Once perfected, this method should eliminate all danger of outbreaks in a district so treated. It would be unnecessary where rain had ceased too early, or begun too late (end January), to permit two generations to be produced in a season.

Application of the method could not be left to local administrative officials and requires expert supervision and some labour and expense, but this would be a small fraction of the cost of measures taken after an outbreak had started.

VI. GENERAL SUMMARY.

Reference should be made to summaries of foregoing sections on pp. 405, 463, and 515.

1. The behaviour of *Schistocerca gregaria* in an outbreak centre on the

Sudanese coast of the Red Sea was observed during 4 months at the beginning of 1937. The investigation was directed towards elucidating the behaviour aspects of the outbreak process.

2. The indigenous, solitary population passed through only one generation in this season, new adults disappearing, perhaps by emigration, in February. No outbreak, therefore, occurred.

3. Three successive immigrant swarms invaded the area. The offspring of the 2nd invasion which did not march away re-populated the cultivation with *dissocians* individuals.

4. The 1st immigrant swarm, despite full gregarious behaviour and coloration, was biometrically nearer to phase *solitaria* than the indigenous population itself. The *dissocians* offspring of the 2nd swarm were biometrically nearer to *gregaria* than either the 1st swarm or the indigenous population.

5. Events leading to an outbreak are divided into 3 stages, which are shown to be practically, as well as theoretically, distinct.

6. The 1st stage is *Concentration*: that is, absolute increase of population density in restricted areas. Two types are distinguished: *Real Concentration* involving actual centripetal movements of the locusts concerned, and *Virtual Concentration* produced by local breeding and resulting in the local increase of population density, without active centripetal movements of the locusts concerned.

7. Real Concentration is a significant quantity, especially in the 1st winter generation. Young hoppers appear not to contribute to it but older hoppers wander, especially in barer zones, and are attracted visually to conspicuous vegetation where they become trapped.

8. Adults are normally less active than older hoppers but under the influence of disturbance contribute something to concentration and are also visually attracted to, and trapped in, the concentration zones.

9. High, moderately dense, irregular vegetation constitutes the concentration zones for hoppers and adults. Unweeded millet was the commonest type of concentration zone but others existed.

10. When a 2nd winter generation is produced the ensuing individuals undergo virtual concentration in the somewhat shrunken concentration zones.

11. The 2nd stage in the outbreak process, termed *Aggregation*, is defined as the grouping of concentrated individuals into immediate contact with one another, and is shown to be produced by the action of external factors acting on each individual separately.

12. In the concentration zones, older hoppers and adults do not remain inactive on the vegetation, but display a diurnal regime resembling in many ways that of phase *gregaria*, determined largely by temperature differences and changes, and involving prolonged basking on the small patches of bare, sheltered and sunlit ground among the vegetation.

13. As the patches are few in relation to number of locusts present, aggregation occurs.

14. The 3rd stage in the outbreak process is termed "*Gregarisation*," that is, the development of typically gregarious behaviour as a result of intensive aggregation.

15. Gregarisation was not observed at Hamashiameb, but comparison of the behaviour of *solitaria*, *gregaria* and *dissocians* locusts indicated that it involved primarily the perfection of the "gregarious instinct" which probably represents a strong tendency to mutual visual "compensation" reactions, and, secondly,

the raising of the whole metabolic, excitation and activity levels, under the combined effect of external and mutual stimulation.

16. The manner in which gregarisation may occur is outlined.

17. Maxwell-Darling's contention that a 2nd winter generation is necessary for an outbreak to occur is confirmed.

18. It is suggested that the Sudanese coastal area may be a complementary part of a larger outbreak area.

19. Tentative proposals are advanced for the permanent control of *Schistocerca* in its outbreak centres.

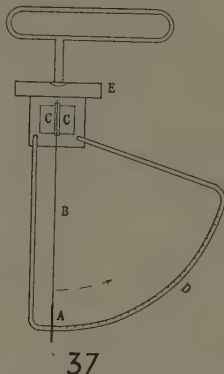


FIG. 37.—“Wind Speed Indicator.”

Appendices.

1. The “Wind Speed Indicator.”

Small airmeters were available giving much more accurate readings than this instrument, but great accuracy in short-time wind measurement has little meaning, and the airmeters suffered from the disadvantage that their vanes were 4 cm. in diameter, the centre of which could not be brought nearer than 5 cm. to the ground. The “Wind Speed Indicator,” based on the Air Speed Indicators used on aeroplanes, made possible rough but rapid wind strength estimation, even near the ground. It consisted (fig. 37) of a vane of card (A) 2.2 cm. square, attached to the lower end of a thin steel strip (B) 10 cm. long and about 4 mm. wide. The upper end of the strip was held in a metal clip (C), which was fastened to a piece of thick cardboard on a wire frame. Part of the wire frame was bent into an arc and nicked (D) to serve as a scale over which the card vane was moved by the wind. A small spirit level (E) was incorporated so as to ensure that no zero error was introduced by tilting.

The vane was viewed edgewise (as in fig. 37), and the approximate maximum and minimum scale readings reached in 10–20 seconds noted. The mean between these two readings gave a figure approximating to that given by an integrating instrument like the airmeter. Calibrations made against an airmeter in the field, and in a wind tunnel, showed a difference probably due to

the observer's paying undue attention to momentary maxima. The former calibration has been used. Between 1.5 and 10 m./sec. the calibration curve is almost straight, two scale divisions out of a total thirty being equivalent to about 1 m./sec. Below 1.5 and above 10 m./sec. the indicator was much less sensitive. Winds of over 10 m./sec. were rare, and winds below 1.5 m./sec. in the field were usually encountered in sheltered places, where the air movement may take irregular and turbulent forms, and cannot be measured by any mechanical instrument known to me. With this proviso, nevertheless, for easy and rapid estimations of wind strengths, quite accurate enough for much ecological work, an instrument like the "Wind Speed Indicator" is possibly a useful suggestion.

2. The Exposure Meter.

Light intensity was measured roughly with a Weston Photographic Exposure Meter (incorporating a Weston Photronic cell), with a range from about 30 to 8000 metre-candles. The intensity from all field sources of light other than the sun itself came within the upper limit of the instrument. Its lower limit prevented its use after the first few minutes of twilight.

This instrument suffered from the great disadvantage that the photo-sensitive surface was covered by a metal diaphragm about 6.5 mm. thick and honeycombed with holes, each 3.9 mm. in diameter and with their centres 4.3 mm. apart. In tests in a parallel light beam the readings were reduced by 50% with the surface of the instrument at 70° to the rays, by 80% at 65°. The instrument was calibrated in front of an electric lamp operated at a colour temperature of 3000° K., a condition not of course strictly comparable with those in the field with surfaces of uneven brightness.

3. Classification of reactions to simple stimuli.

The term tropism, with various prefixes, is frequently employed in locust literature. For its history and an account of the chaos in its use, reference should be made to Mast (1911, 1915, 1938), Kühn (1919) and Fraenkel (1931). It is often used as a blanket term covering any apparent correlation between behaviour and external factors, so that it is impossible to tell whether it is to be understood as purely descriptive or explanatory, as indicating a directed or undirected relation to the stimulus. Distinction between the various types of reaction (below) may be very important, as circumstances may make it impossible for one or other type to operate, correlation having therefore nothing to do with causation. Several examples of this have occurred in this paper, on pp. 435, 461, 493, 520.

To simple descriptions of behaviour the term tropism adds nothing; as a physiological term it is meaningless. Its continued use in accounts of locust behaviour is an obstacle to progress in the understanding of that behaviour.

In this paper the Kühn (1919) system of classification of simple behaviour types has been largely used, because, so long as it is recognised as makeshift only, some classification is desirable in reaction types, for these are at a higher organisational level than reflex physiology. For the convenience of readers, a brief résumé of the main types will be given here, largely taken from Fraenkel (1931).

KINESIS.

Variations in the intensity of the stimulus produce variations in the rate of random locomotion. The direction of locomotion bears no relation to the

direction of a stimulus gradient or of a radiant source. In a positive kinesis locomotion rate increases with intensity of stimulus, and vice versa. Thus in positive photokinesis animals become more active in brighter light, and consequently collect in a region of dimmer light.

TAXIS.

The stimulus affects the direction taken by the animal, apart from the latter's locomotion rate. A taxis is positive when it results in movement into a region where the stimulus is stronger.

Phobotaxis :

"Orientation in an undirected path." Changes in the intensity of the stimulus evoke "avoiding reactions," and "according as the avoiding reaction is a result of a stimulus above or below the optimal intensity the organism is eventually forced to move away from or towards the source of stimulation." The weakness of this term is readily apparent (Gunn, Kennedy and Pielou, 1938), and a phobotaxis cannot be described as positive or negative.

Topotaxis :

"The movement is directed in respect to the source of stimulation. The following varieties of directed reaction are to be distinguished" :

Tropotaxis : "orientation in an excitation equilibrium for symmetrically placed receptors and a tonus equilibrium for symmetrically placed effectors."

Distinguishing features : (i) circus movements after unilateral extirpation of sense organs, (ii) resultant position taken up in relation to more than one source of stimulation.

Telotaxis : "the assumption of a position so that a certain region of the receptor apparatus is acted upon by the stimulus. Definite turning reflexes are linked up with the stimulation of each point of the receptor apparatus. These vary with the strength and direction of the stimuli. The resulting movement is either directly towards or away from the source of stimulation."

Distinguishing features : (i) no circus movements after unilateral extirpation of sense organs, (ii) no resultant position in relation to more than one source of stimulation; one source is dominant to the exclusion of others.

Menotaxis : "maintaining a definite angle between the direction of motion and the line joining the source of stimulation with the sense organ."

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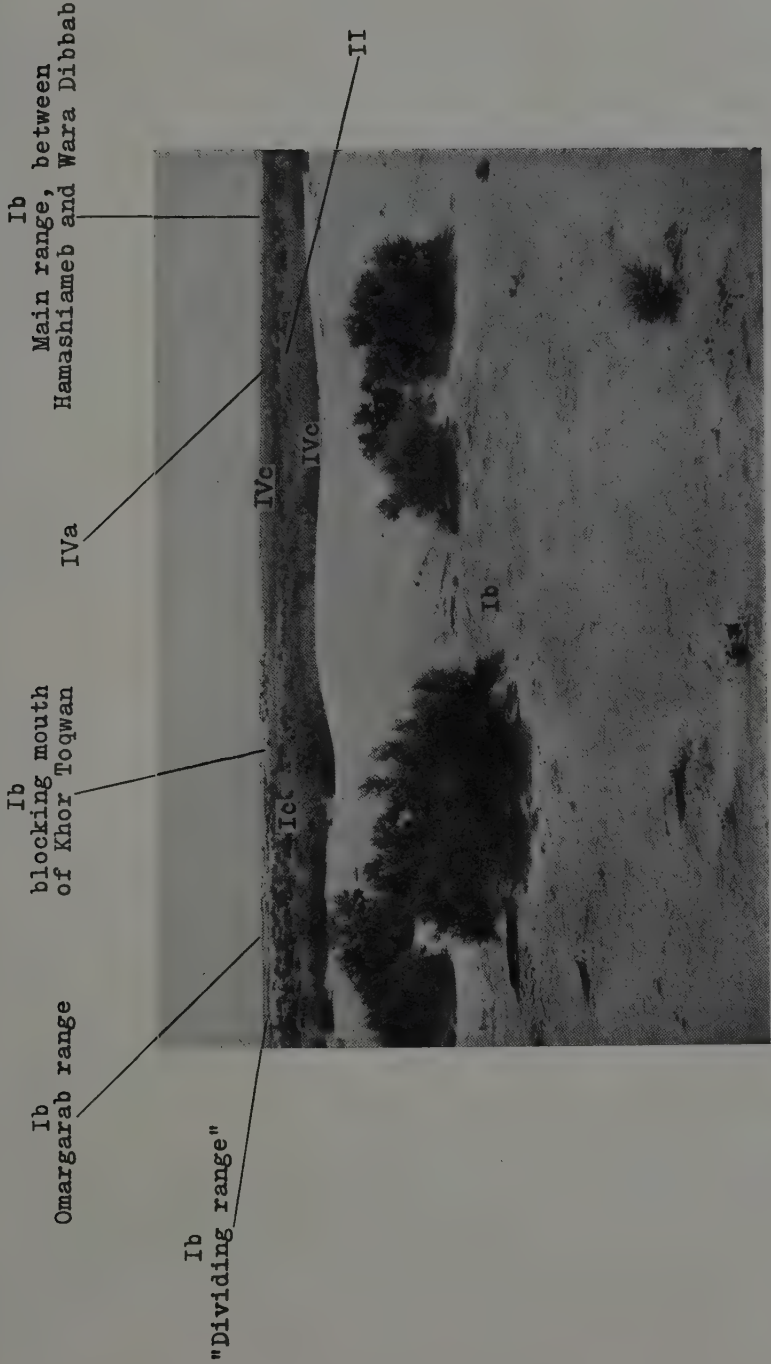
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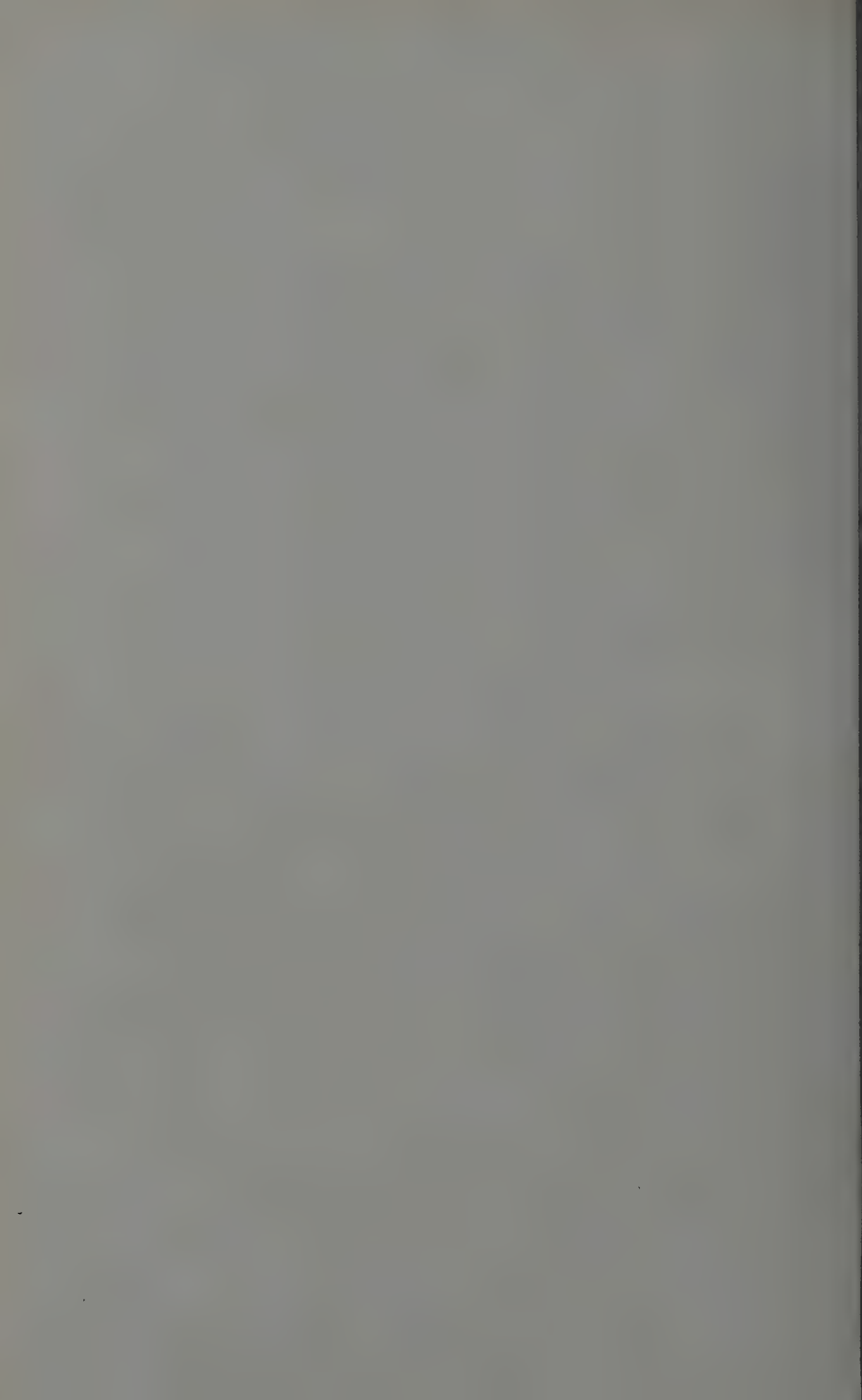
EXPLANATION OF PLATES.

- PLATE 1, fig. 1.—General view from the north end of the cultivated part of Khor Toqwan, looking south-south-west, February. Various dune ranges and vegetation zones marked (see map, fig. 1, and pp. 389-390).
- PLATE 2, fig. 2.—Zone Ia, the open flood-plain, between the camp and La'at. March. Small *Suaeda* bushes, and scattered tufts of grass, etc. The vegetation merges into zone Ic type in the background.
Locusts of all stages very rare. Average rate of daily travel of 5th instar hoppers, 122 m. The man is engaged in "stalking" a hopper during the three-day wandering experiments.
- PLATE 2, fig. 3.—Zone Ib, the sand dunes near north end of cultivated part of Khor Toqwan. March. Large *Suaeda* (right) and *Panicum* (left) bushes.
Locusts of all stages very rare. Average rate of daily travel of 5th instar hoppers, 87 m. White labels left to mark hoppers' path (leading to bush) in half-hour wandering experiments.
- PLATE 3, fig. 4.—Zone Ib', a large "mat" of *Heliotropium undulatum* among the marginal dunes near to cultivation (in background), west-north-west of the camp. February. Matting shelter for recording instrument in centre, about 40 cm. high.



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General View of Khor Toqwan.





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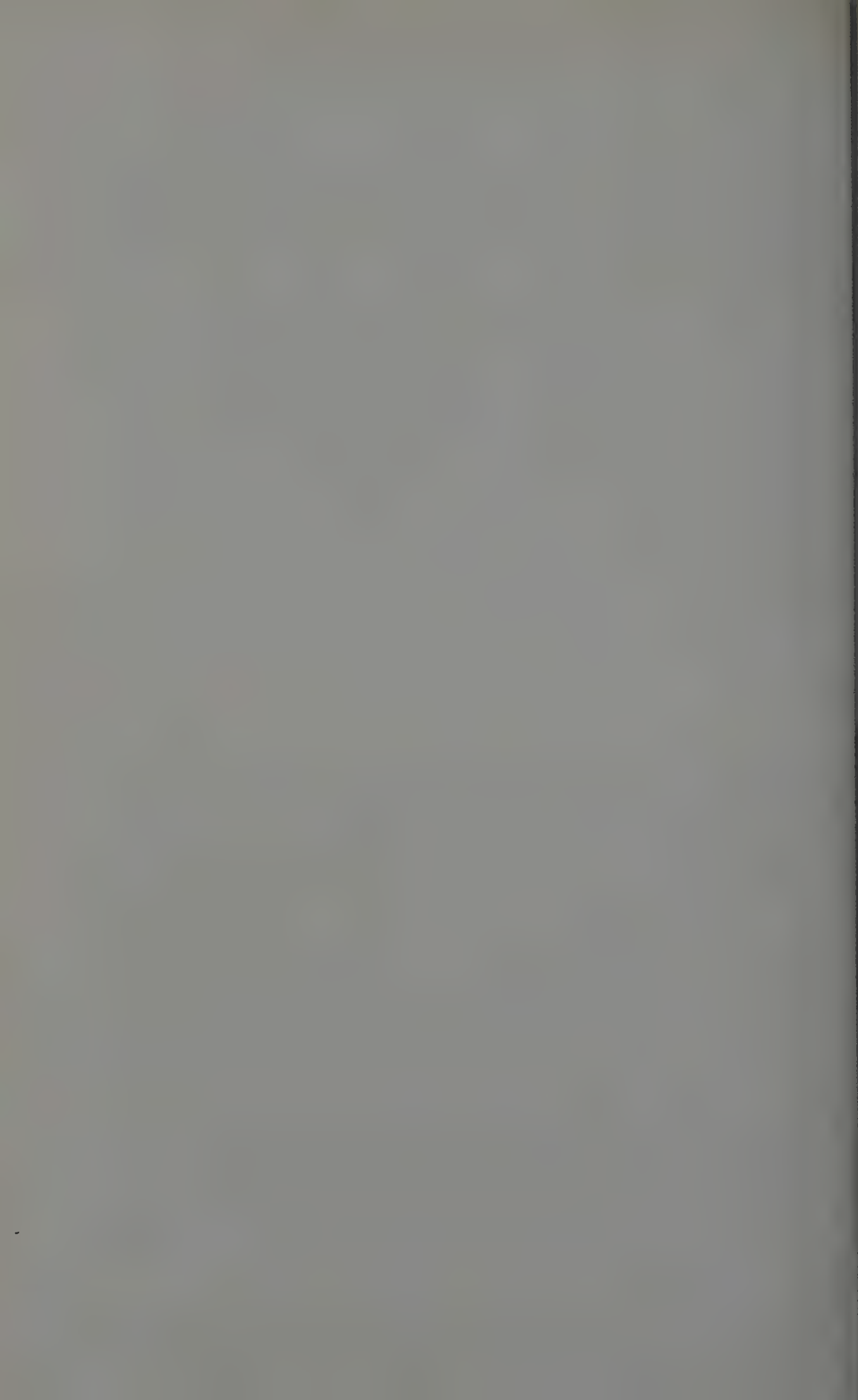
Zone Ia and Zone Ib.





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Zone Ib and Zone II.





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Zone III.



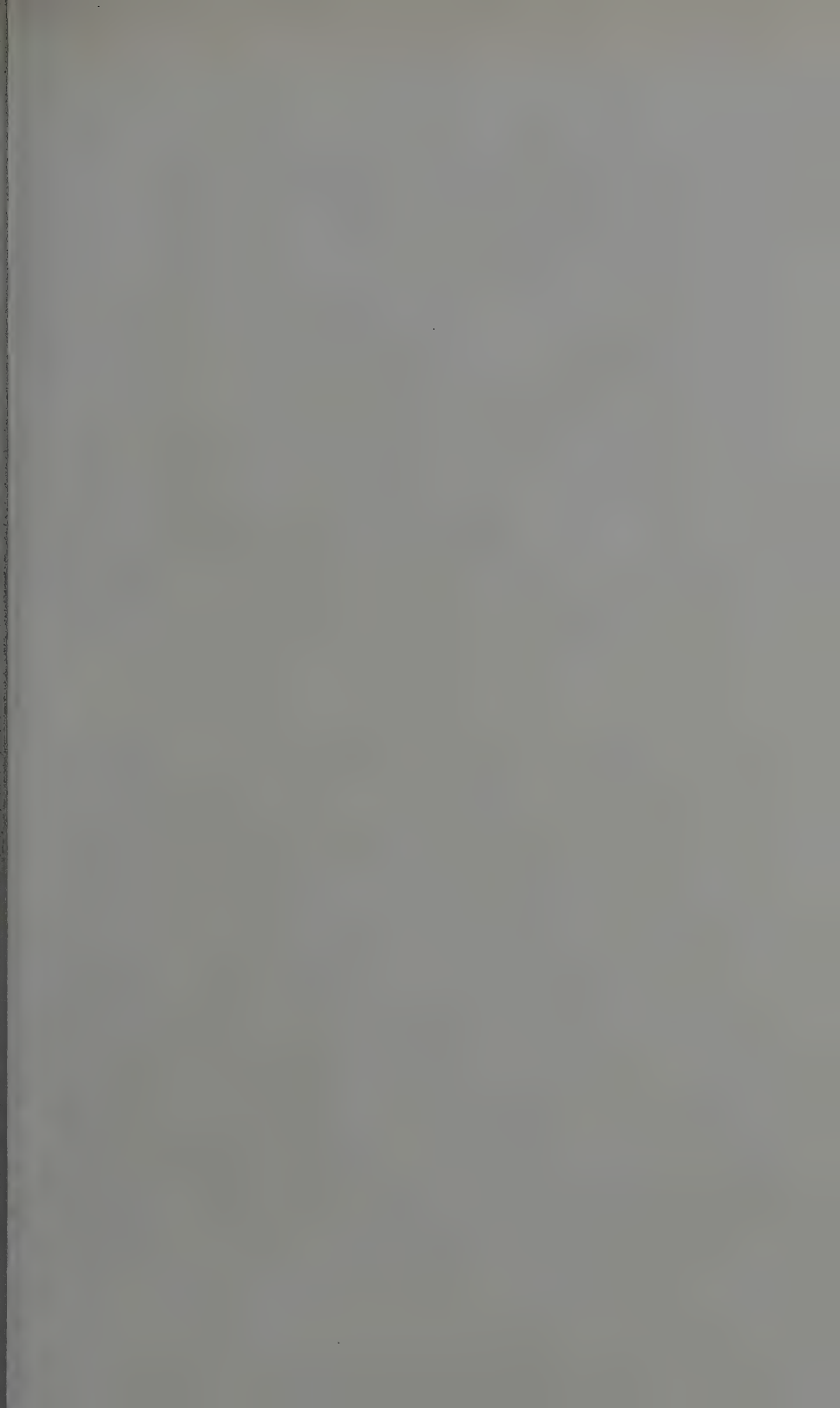
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Zone IVa and Zone IVb.



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Zone IVb and Zone Ic.





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Young hoppers very numerous. Older hoppers tend to wander away, but while present come down and bask on the ground, sometimes forming groups, particularly along the lee edge of the "mat." Adults rare.

PLATE 3, fig. 5.—Zone II, continuous dense grass near north end of cultivated part of Khor Toqwan. March. In this case with scattered, thin millet stands, and *Suaeda* bushes bordering.

Young hoppers numerous. Older hoppers tend to wander and collect where bare sheltered ground or millet is encountered. Average rate of stimulated half-hour's travel, 2.2 m. No aggregation. Some adults present, but tend to scatter. White labels left to mark hopper's path in half-hour wandering experiments.

PLATE 4, fig. 6.—Zone III, irregular low vegetation (foreground), Wara Dibbab. March. *Suaeda* bushes, grasses, *Heliotropium pallens*, etc. This is an example of "poor" zone III, somewhat dried out; undergrowth between bushes often more luxuriant and irregular.

Young hoppers numerous. Older hoppers also numerous, unless millet is adjacent to attract them away. Basking on any sheltered ground, sometimes with small group formation in lee of bushes. Some adults present, but tend to scatter when hardened.

PLATE 4, fig. 7.—The margin of an area of zone III of a special type (zone Ia on left, and man in background), Wara Dibbab. Large discrete *Suaeda* bushes on mounds, with grass and *Heliotropium pallens*. March.

Young hoppers numerous. Older hoppers numerous and collect on bushes, forming large basking groups on lee side of each mound. Adults also quite numerous, but less aggregated than hoppers.

PLATE 5, fig. 8.—Zone IVa, large *Suaeda* bushes densely packed, with grass and other weeds, and bare ground interspersed, south-south-west of camp. March.

A "concentration zone" for locusts of all stages as long as undergrowth remains green, with aggregation of older hoppers and adults on sheltered bare patches.

PLATE 5, fig. 9.—Zone IVb, millet without weeds, west-north-west of camp. January.

Young hoppers few. Some older hoppers (but collect in millet with undergrowth if available), basking on ground mostly singly, only small groups being formed. Adults numerous, but little aggregated.

PLATE 5, fig. 10.—Same as pl. 5, fig. 9, towards the end of April, after harvesting and the admission of cattle.

Adults collect along downwind edges of such patches.

PLATE 6, fig. 11.—Zone IVb, close-up view of interior of millet without weeds, beginning to wither, in mouth of Khor Toqwan. March. Including two of the small wooden screens used in micro-climatic records on 27.iii. (position A and another).

PLATE 6, fig. 12.—Foreground: Zone Ic, larger *Suaeda* bushes and more undergrowth than zone Ia. Middle background: a strip of zone IVc, an unusual example of millet cultivation choked with large *Suaeda* bushes and grass, but including bare patches. At the extreme northern end of the cultivated part of Khor Toqwan. February.

This illustrates the normal condition in which "concentration zones" are sharply demarcated from adjoining zones, and can thus serve as powerful visual attractants for hoppers and adults (see also pl. 1, fig. 1; pl. 3, fig. 4; and pl. 4, fig. 7).

PLATE 7, fig. 13.—Close-up of the interior of typical zone IVc, millet with weeds and interspersed bare patches, northern half of cultivation in Khor Toqwan. February. Showing the wooden shade and "sun thermometer" at position B of the micro-climatic records on 16.ii.

Zone IVc was the principal concentration zone for locusts of all stages, and older hoppers and adults became aggregated on the bare patches.

PLATE 7, fig. 14.—Zone IVc, showing position C of the records on 16.ii.

A. roof of wooden shade; B. "sun thermometer" with bulb projecting free of wood; C. shade thermometer with bulb under roof; D. Edney paper hygrometer suspended from roof.

PLATE 8, fig. 15.—Zone IVc, a typical small basking-place where aggregation of older hoppers and adults occurred. Position D of the records on 16.ii.

A. matting shade over bulb of shade thermometer and paper hygrometer;

B. soil surface thermometer. "Sun thermometer" present but not showing.

PLATE 8, fig. 16.—Zone IVc, a clearing among unweeded millet, showing the shades and instruments of positions B₁ and D₁ of the records on 16.ii.

Adults bask anywhere on such bare ground, but hoppers keep close to undergrowth along the edges.

PLATE 9, fig. 17.—Arrangement for experiments on visual attraction of hoppers to vegetation.

A. observer looking through peep-hole in box; B. bush attached to front of box; C. circular piece of rush matting, covering pit containing assistant with stock of hoppers; D. twig projecting through hole in centre of matting, through which hoppers climbed; E. compass points, and circle with centre at D, marked on ground.

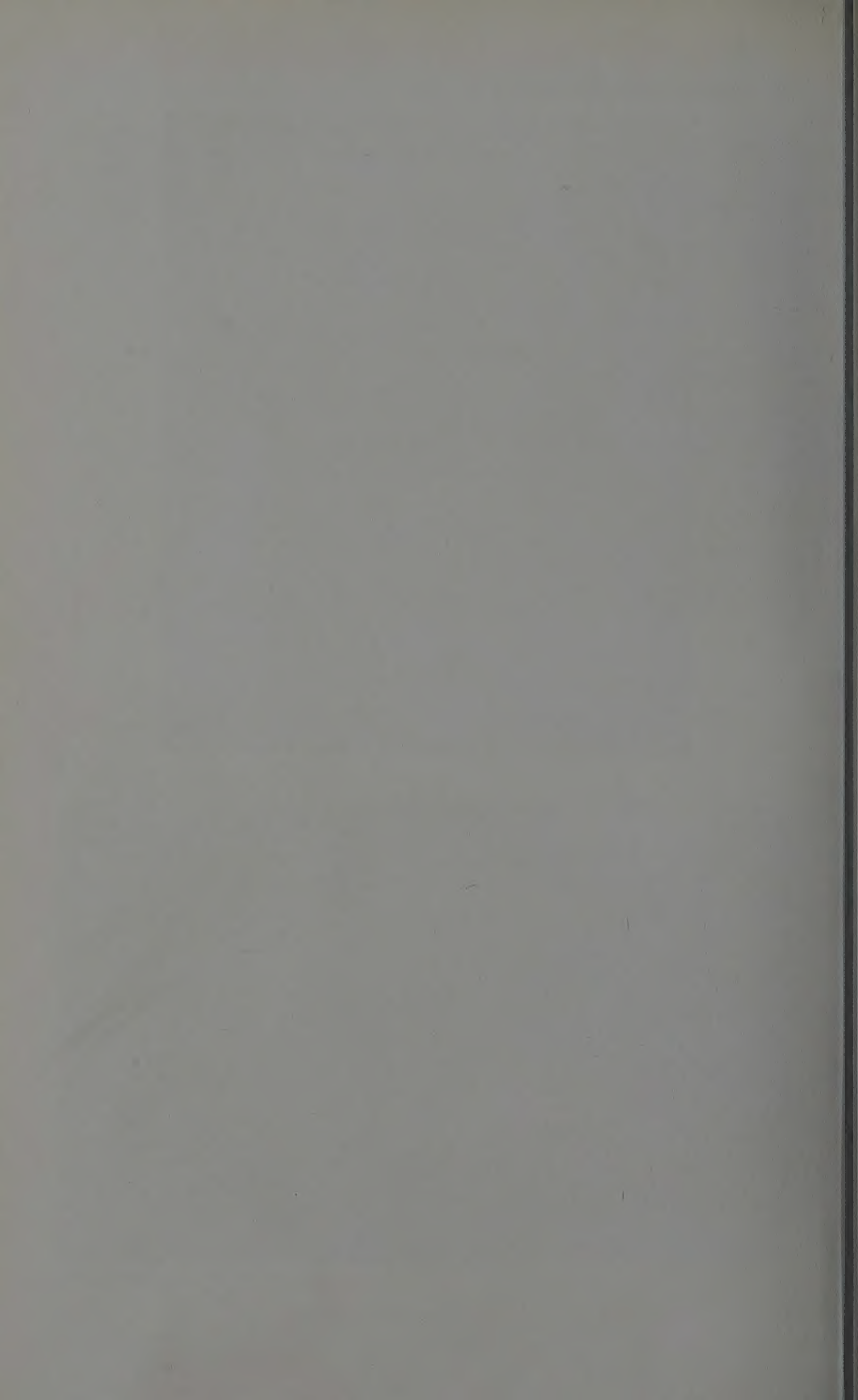
PLATE 9, fig. 18.—Arrangement for experiments on the effects of rapid temperature changes on hopper activity.

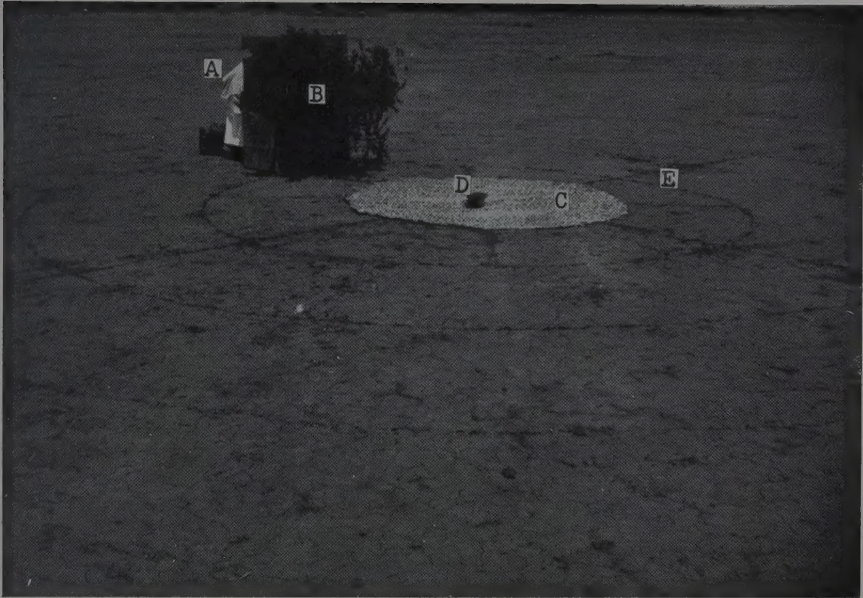
Observer with head at X, noted body temperature of a hopper on a thermocouple needle in cage A, and number of hoppers moving in cage B. W. wind screen; S. sun screen (in lowered position). Sun falling from right during experiments, not as shown.



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Zone IVc.





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Experiments on visual attraction, and the effect of rapid temperature change.

